

ABUNDANCE AND POTENTIAL YIELD OF THE ROUND HERRING, *ETRUMEUS TERES*, AND ASPECTS OF ITS EARLY LIFE HISTORY IN THE EASTERN GULF OF MEXICO¹

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ABSTRACT

Eggs and larvae of the round herring, *Etrumeus teres*, were surveyed from plankton collections made in the eastern Gulf of Mexico from 1971 to 1974 to determine adult stock size, spawning areas, and spawning seasons and to study aspects of its early life history. Spawning occurred from mid-October through May where depths ranged from 30 to 200 m, surface temperatures from 18.4° to 26.9°C, and surface salinities from 34.5 to 36.5‰. A major spawning area was present 150 km from Tampa Bay between lat. 27°00' and 28°00'N and long. 083°30' and 084°30'W. Mean relative fecundity of 8 adult females was 296.5 ova per gram and the sex ratio of 71 adults was 1:1. The development time of eggs from spawning to hatching was approximately 2.0 days at 22°C. Three methods were used to determine adult biomass. The most probable annual estimates of biomass were approximately 700,000 metric tons in 1971-72 and 130,000 metric tons in 1972-73. The best estimates of the range of potential annual yields to a fishery were from 50,000 to 250,000 tons. Abundance and mortality rates of larvae were estimated in each year. It is probable that more than 99.4% mortality occurred between spawning and the 15.5-mm larval stage during 31 days in 1971-72 and more than 98.3% mortality occurred for the same period in 1972-73.

Round herring, *Etrumeus teres* (DeKay), is one of several clupeid fishes that are abundant in continental shelf waters of the eastern Gulf of Mexico. Distribution and abundance of this species was determined, based on egg and larvae surveys, as part of a program to investigate abundance and fishery potential for sardinelike fishes in the eastern Gulf. It is generally believed that several species of underexploited clupeid fishes from this area could provide significant catches (Bullis and Thompson 1967; Bullis and Carpenter 1968; Wise 1972) that would supplement yields of the heavily exploited Gulf menhaden, *Brevoortia patronus*. The egg and larvae surveys were carried out in 17 cruises from 1971 to 1974. Preliminary reports on clupeid abundance, based on these surveys, have been published (Houde 1973a, 1974) and overall results of the surveys were recently summarized (Houde 1976; Houde et al. 1976; Houde and Chitty 1976).

There are eight apparently discrete populations of *Etrumeus* in the world oceans. Whitehead (1963) has placed all of the forms in the single species *E. teres*. Recorded populations occur in the

western Atlantic from Cape Cod into the Gulf of Mexico, in the eastern North Pacific from the Gulf of California to north of Los Angeles, in the central North Pacific near Hawaii, in the Indo-Pacific off the south and west coasts of Australia, in the western North Pacific off the coasts of Japan, in the western Indian Ocean off the east coast of South Africa, in the Red Sea, and near the Galapagos Islands in the Eastern Pacific.

Eggs and larvae of *E. teres* have been described from some areas where they occur (Blackburn 1941; Uchida et al. 1958; Mito 1961; Houde and Fore 1973; O'Toole and King 1974; Watson and Leis 1974). Ito (1968) examined fecundity and maturity of round herring from the Sea of Japan. Spawning by Hawaiian round herring recently was discussed by Watson and Leis (1974). Distribution and abundance of round herring eggs and larvae were reported in the Gulf of California (Moser et al. 1974; De la Campa de Guzman and Ortiz Jimenez 1975) and in the northern Gulf of Mexico by Fore (1971). Khromov (1969) found *Etrumeus* larvae to be common in plankton catches during a winter survey of the eastern Gulf of Mexico.

Round herring are fished commercially off Japan and South Africa. A catch of approximately 26,000 metric tons was made by South Africa in 1973 (Food and Agriculture Organization 1974;

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O'Toole and King 1974), and the Japanese catch was 40,400 metric tons in that year (Food and Agriculture Organization 1974). The species is not fished at present in the Gulf of Mexico. Salnikov (1969) reported that round herring was abundant in the northeastern Gulf of Mexico, and Harvey Bullis (pers. commun.) stated that it was plentiful in the eastern Gulf, based on acoustic traces and trawl catches made by National Marine Fisheries Service research vessels. Our initial surveys of eggs and larvae indicated that it might be abundant in the eastern Gulf (Houde 1973a), and Fore (1971) reported round herring eggs and larvae to be abundant in the northern Gulf of Mexico. In the absence of a commercial fishery, catch and effort statistics, and other data on abundance, I have estimated the adult biomass in the eastern Gulf from the abundance of eggs that were spawned annually. This fishery-independent technique of biomass estimation can provide preliminary knowledge of fishery potential (Ahlstrom 1968) and is considered to be a useful biomass estimating procedure (Saville 1964; Smith and Richardson in press).

METHODS

Survey Area and Times

Seventeen plankton surveys were made in the eastern Gulf of Mexico between lat. $24^{\circ}45'$ and $30^{\circ}00'N$ (Figure 1) in 1971-74 (Table 1). Most sampling stations were located on the broad continental shelf, where depths ranged from 10 to 200 m, but a few stations were over the continental slope where depths were greater. Potential sampling stations were on transects running parallel to lines of latitude; transects were spaced at 15-nautical-mile (27.8-km) intervals. Stations were located at 15-mile (27.8-km) intervals on each transect, except for those stations beyond the 200-m depth contour, which were placed at 30-mile (55.6-km) intervals (Figure 1). Not all stations were sampled on each cruise (Table 1). Other details of survey planning and design have been reported elsewhere (Rinkel 1974; Houde et al. 1976; Houde and Chitty 1976).

Beginning with cruise IS 7205 (Table 1), sampling was restricted to stations on alternate transects. The three stations nearest to shore (at 27.8-km intervals) were sampled on each of the designated transects but only stations at 30-mile (55.6-km) intervals were sampled offshore. A few

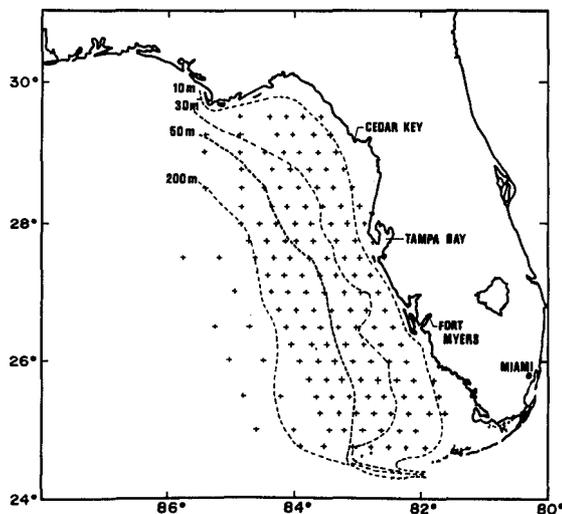


FIGURE 1.—Area encompassed by the 1971-74 eastern Gulf of Mexico ichthyoplankton surveys. Plus symbols (+) represent stations that were sampled during the survey. The 10-, 30-, 50-, and 200-m depth contours are indicated.

additional stations were added on 1974 cruises in areas where depth was less than 10 m; no round herring eggs or larvae occurred at these stations and they were not important with regard to spawning by this species, but they were important in determining spawning and distribution of other Gulf clupeids.

Plankton Sampling

A paired 61-cm Bongo net plankton sampler was used on all cruises except cruise GE 7101, in which a 1-m ICITA [International Cooperative Investigations of the Tropical Atlantic (Navy)] plankton net with 505- μm mesh was towed. Meshes on the Bongo sampler were 505 μm and 333 μm . Ichthyoplankton was sorted from the 505- μm mesh net and plankton volumes were determined from the 333- μm mesh net catch (Houde and Chitty 1976). Net tows were double oblique from within 5 m of bottom to surface or from 200-m depth to surface at deep stations. Nets were towed at approximately 3.0 knots (1.5 m/s) in 1971, but towing speed was reduced on later cruises and averaged 2.3 knots (1.2 m/s) (Table 2). Stations were sampled whenever the ship occupied them; thus, tows were made during either daylight or darkness, depending on the time of arrival at a station.

Prior to cruise GE 7208, all tows consisted of

TABLE 1.—Summarized data on cruises to the eastern Gulf of Mexico, 1971-74, to estimate abundance of round herring eggs and larvae. (GE = RV *Gerda*, 8C = RV *Dan Braman*, TI = RV *Tursiops*, 8B = RV *Bellows*, IS = RV *Columbus Iselin*, CL = RV *Calanus*.)

Cruise	Dates	Number of stations	Positive stations for eggs ¹	Positive stations for larvae ²	Mean egg abundance under 10 m ²		Mean larvae abundance under 10 m ²	
					All stations	Positive stations	All stations	Positive stations
GE 7101 ³	1-8 Feb. 1971	20	4	9	39.37	196.88	7.34	16.30
8C 7113								
TI 7114	7-18 May 1971	123	2	24	0.21	12.88	3.00	15.80
GE 7117	26 June-4 July 1971	27	0	0	0.00	—	0.00	—
8C 7120								
TI 7121	7-25 Aug. 1971	146	0	0	0.00	—	0.00	—
TI 7131								
8B 7132								
GE 7127	7-16 Nov. 1971	66	15	20	41.41	187.73	4.18	14.20
8B 7201								
GE 7202	1-11 Feb. 1972	30	8	13	151.20	604.81	20.29	49.97
GE 7208	1-10 May 1972	30	2	2	1.38	22.11	0.28	4.44
GE 7210	12-18 June 1972	13	0	0	0.00	—	0.00	—
IS 7205	9-17 Sept. 1972	34	0	0	0.00	—	0.00	—
IS 7209	8-16 Nov. 1972	50	5	2	0.83	8.30	1.61	40.28
IS 7303	19-27 Jan. 1973	51	12	20	23.77	101.04	19.12	48.76
IS 7308	9-17 May 1973	49	2	3	2.48	60.72	2.29	37.41
IS 7311	27 June-6 July 1973	51	0	0	0.00	—	0.00	—
IS 7313	3-13 Aug. 1973	50	0	0	0.00	—	0.00	—
IS 7320	6-14 Nov. 1973	51	8	5	4.11	26.22	1.11	11.32
CL 7405 ⁴	28 Feb.-9 Mar. 1974	36	0	0	0.00	—	0.00	—
CL 7412	1-9 May 1974	44	1	1	0.49	21.50	3.98	175.07

¹Positive station is a station at which round herring eggs were collected.

²Positive station is a station at which round herring larvae were collected.

³An ICITA, 1-m plankton net was used on this cruise. On all other cruises a 61-cm Bongo net was used.

⁴No stations in offshore areas were sampled, accounting for the failure to collect round herring eggs or larvae on this cruise.

TABLE 2.—Summary of plankton tow characteristics for 17 ichthyoplankton cruises to the eastern Gulf of Mexico. The 61-cm Bongo net sampler was used on all cruises except GE 7101 in which a 1-m ICITA net was used.

Cruises	Number of stations	Mean volume filtered (m ³)	Standard error of volume filtered (m ³)	Mean towing speed (m/s)	Standard error of towing speed (m/s)	Mean volume filtered per unit depth (m ³ /m)	Standard error of volume filtered per unit depth (m ³ /m)
GE 7101	20	675.25	30.29	—	—	49.69	11.58
8C 7113 & TI 7114							
GE 7117							
8C 7120 & TI 7121	358	160.17	7.27	1.44	0.03	3.60	0.11
8B 7132 & TI 7131							
GE 7202 & 8B 7201							
GE 7208							
GE 7210							
IS 7205	335 <55 m deep	104.39	0.92	1.17	0.01	11.04	0.57
IS 7209							
IS 7303							
IS 7308							
IS 7311							
IS 7313							
IS 7320	124 >55 m deep	231.93	11.80	1.18	0.01	2.37	0.07
CL 7405							
CL 7412							

wire release at 50 m/min to desired depth and retrieval at 20 m/min. In later cruises, two types of tow were used, a shallow-water tow at stations less than 55 m deep and the usual 50 m/min release-20 m/min retrieval tow at deeper stations (Table 2). The shallow-water tow was of 5-min duration; it consisted of 1 min for wire release and 4 min for wire retrieval. The objective at shallow stations was to filter 100 m³ of water. This objective was met, but the volume of water filtered per unit of depth fished by the net was increased significantly at the shallow stations relative to deeper stations

(Table 2). This discrepancy in type of tow was considered to be more desirable than the alternative situation, which existed in 1971, when as little as 25 m³ of water were filtered at some of the shallowest stations. Tows at stations deeper than 55 m filtered between 100 and 400 m³.

A stopwatch was used to monitor each tow and the wire angle was measured at the end of each minute of a tow. A time-depth recorder gave a record of tow characteristics. Volume filtered was determined from a flowmeter in the mouth of the 505- μ m mesh net.

Plankton Samples

All samples were preserved immediately in 10% seawater Formalin³ buffered with marble chips. Samples were transferred to 5% buffered Formalin after they had been stored in the laboratory for 1 mo. Houde and Chitty (1976) have discussed methods used to determine plankton volumes. All fish eggs and larvae were sorted from each 505- μm mesh net plankton sample under a dissecting microscope for later identification and enumeration.

Eggs and larvae of round herring are distinctive and easily identified (Houde and Fore 1973). Round herring eggs from each station were enumerated; larvae were enumerated and measured with an ocular micrometer in a dissecting microscope.

Temperatures and Salinities

Temperature and salinity profiles of the water column at each station were obtained on all cruises.⁴ Usually a mechanical bathythermograph cast was made to describe the vertical temperature profile. This was followed by a hydrocast consisting of from two to seven 1.7-liter Niskin bottles with reversing thermometers. Samples for salinity were brought to Rosenstiel School of Marine and Atmospheric Science for analysis. On cruises IS 7308 and IS 7320 a salinity-temperature depth unit was used in place of the Niskin bottles to obtain temperature and salinity data. Round herring egg and larva data were examined in relation to temperatures and salinities at stations where they were collected.

Determining Egg and Larvae Abundance

Catches of round herring eggs and larvae at each station were standardized to give abundance in numbers under 10 m² of sea surface:

$$n_j = \frac{c_j z_j}{v_j} \cdot 10 \quad (1)$$

where n_j = the number of individuals (eggs or larvae) at station j under 10 m² of sea surface

c_j = the catch of eggs or larvae at station j
 z_j = the depth of tow (in meters) at station j
 v_j = the volume filtered by the net (in cubic meters) at station j .

Both total larval abundance under 10 m² and larval abundance in each 1.0-mm length class under 10 m² were determined.

Numbers of eggs or larvae also were estimated in the area represented by each station. These areas were determined by the polygons described by the perpendicular bisectors of lines from the station in question to adjacent stations (Sette and Ahlstrom 1948):

$$p_j = \frac{c_j z_j}{v_j} \cdot A_j \quad (2)$$

where p_j = the estimated total number of eggs or larvae in the area represented by station j

c_j , z_j , and v_j are defined in Equation (1)
 A_j = the area (in square meters) represented by station j .

Total larvae and larvae by 1.0-mm length classes were estimated for each station area. Most stations represented areas ranging from 0.75 to 3.15 $\times 10^9$ m².

The estimated total number of eggs and larvae, as well as larvae by 1.0-mm length classes, was estimated for the entire area represented by each cruise:

$$P_i = \sum_{j=1}^k p_j \quad (3)$$

where P_i = the cruise estimate (i.e., the total number of eggs or larvae estimated in the area represented by cruise i)

k = the number of stations sampled during cruise i

p_j is defined by Equation (2).

Variance estimates on the abundance of eggs were obtained for each cruise using a combination of methods outlined by Cushing (1957) and Taft (1960). Only stations at which round herring eggs had been collected at least once during the 1971-74 survey period were included in obtaining these estimates. Other stations were considered to be outside the area of spawning, because round herring eggs were never collected there. These usually were the three stations on each transect that

³Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

⁴Temperature and salinity data for these cruises can be retrieved from the MAFLA file at the National Oceanographic Data Center, Washington, D.C.

were located closest to the coast (Figure 1). An estimate of the variance in egg abundance under a square meter of sea surface (s_{ij}^2) was obtained from the $\log_{10}((c_{jz_j})/v_j) + 0.1$ egg catch at each station during a cruise (Cushing 1957). The \log_{10} variance estimate so obtained was backtransformed to obtain the untransformed estimate of variance. The variance estimate for a cruise was calculated using the estimator given by Taft (1960) that assumes random sampling. It is:

$$S_{P_i}^2 = D_i^2 \sum_{j=1}^{k_i} \frac{A_{ij}^2 s_{ij}^2}{d_{ij}^2} \quad (4)$$

where $S_{P_i}^2$ = variance estimate on the abundance of eggs spawned during the period represented by cruise i

D_i = the number of days represented by cruise i , defined as the days included in the cruise plus one-half the days since the previous cruise and one-half the days to the next cruise (Sette and Ahlstrom 1948). When a cruise took place shortly after the assumed date of the beginning of the round herring spawning period (15 October) or near the end of the spawning season (31 May), the number of days from the inclusive cruise days to the beginning or end of the season was used in estimating D_i

A_{ij} = the area (m^2) represented by the j th station in the i th cruise

d_{ij} = the duration (days) of the egg stage from spawning until hatching. The best estimate of d_{ij} for round herring is 2.0 days, based on observed egg stages in catches during the surveys and this value was used in all abundance and variance calculations

s_{ij}^2 = the variance estimate for the number of eggs present under $1 m^2$ of sea surface for cruise i

k_i = the number of stations included in the variance estimate for cruise i .

Sampling was not random in the eastern Gulf surveys. Also, egg catches were not normally or log-normally distributed, nor did the distribution of catches fit contagious distributions like the negative binomial. Thus, the variance estimates that I have obtained are not the best estimates, but

they may be reasonable approximations (Saville 1964) for variance in the area represented by the cruises. Variation in spawning that occurs over time (i.e., day to day variation) has not been accounted for, which is the usual situation in ichthyoplankton abundance surveys (Saville 1964).

An estimate of the abundance of eggs spawned over the entire spawning season is:

$$P_a = \sum_{i=1}^r \frac{P_i D_i}{d_i} \quad (5)$$

where P_a = the total number of eggs spawned in an annual spawning season

r = the number of cruises upon which the estimate of annual spawning is based
 P_i , D_i , and d_i are defined in Equation (4).

An estimate of variance on the number of eggs spawned annually was obtained, assuming that sampling was random using the formula given by Taft (1960):

$$S_{P_a}^2 = \sum_{i=1}^r S_{P_i}^2 \quad (6)$$

where $S_{P_a}^2$ = the variance estimate on the number of eggs spawned annually

r is defined in Equation (5)

$S_{P_i}^2$ is defined in Equation (4).

This variance estimate, like that for individual cruise abundance estimates, is not entirely satisfactory because the assumptions of random sampling and normally distributed catches do not hold. Also, as in the cruise variance estimates (Equation (4)), it was not possible to obtain an estimate of variance in abundance due to day to day variability, thus leaving variation in time unaccounted. Taft has shown that this can be a large source of error and that annual spawning estimates will not be more precise than individual cruise estimates when variation in time is not considered.

Biomass Estimating Procedure

An estimate of adult biomass of a fish stock can be obtained if the annual spawning (number of eggs), sex ratio, and relative fecundity (eggs produced per gram adult female per year) are known (Saville 1964; Ahlstrom 1968). Biomass of adults is:

$$B = \frac{P_a}{F_r \cdot K} \quad (7)$$

where B = biomass of adults in the stock

F_r = mean relative fecundity of females
(eggs produced per gram female per year)

K = the proportion of adults that are females

P_a is defined in Equation (5).

Estimates of P_a , F_r , and K were obtained for round herring in the Gulf of Mexico.

An estimate of K was derived from examination of 71 gonads of adult round herring trawled from the Gulf of Mexico by the National Marine Fisheries Service. The estimate of F_r also was obtained from these specimens. Fecundity was estimated by the gravimetric method (Holden and Raitt 1974). Modes of yolked oocytes were assumed to be spawned during an annual spawning cycle. This assumption was supported by the presence of only a single mode of unyolked oocytes in six females collected during months when no spawned eggs were collected in plankton tows. Fecundity was estimated in a sample of eight near-ripe females. Procedures used to estimate round herring fecundity are like those outlined for scaled sardine, *Harengula jaguana*, by Martinez and Houde (1975).

Three techniques were used to estimate adult biomass. All give estimates of annual spawning (P_a) that are based on the same egg catches, standardized per unit area of sea surface. Thus, the three estimates of biomass for each spawning season are not independent; but, because each technique has unique assumptions, the spawning estimates are different, and it was useful to calculate biomass by each procedure for comparison purposes. The three techniques are outlined by Sette and Ahlstrom (1948), Simpson (1959), and Saville (1956, 1964).

The method first used by Sette and Ahlstrom (1948) and subsequently by Ahlstrom (1954, 1959a) is based on obtaining an estimate of annual spawning by the techniques that I have outlined in Equations (2), (3), (5), and (7). It assumes that the abundance of eggs at a station is equal over the entire area represented by that station. Moreover, it assumes that egg abundance at the time of collection is the same on each day of the cruise period and also for one-half the days since the preceding cruise, or since the beginning date of the spawning

season plus one-half the days until the next cruise or the number of days until the end of the spawning season.

Simpson's (1959) method was modified to obtain round herring annual spawning estimates. He obtained his estimates of spawning during each cruise by summing areas within contours of egg abundance. I used Equation (3) to obtain cruise estimates. The annual spawning estimate (P_a) was obtained by plotting the daily spawning estimate for each cruise (P_i/d_i) against the middate of the cruise (Simpson 1959). The area under the resulting polygon was obtained by planimeter and was equated to annual spawning. Because Equation (3) was used to obtain cruise spawning estimates, Sette and Ahlstrom's (1948) and Simpson's (1959) methods give results that converge, the two annual spawning estimates differing only by some number of eggs spawned near the beginning and near the end of the spawning season. The Sette and Ahlstrom technique will always give a somewhat larger estimate of annual spawning for species like round herring that have a well-defined spawning season, but identical estimates will result for species that spawn year round.

The third method (Saville 1956, 1964) assumes that spawning follows some known distribution during the season. Spawning is approximately normally distributed throughout the season for many fishes. Thus, cruises that fall within the spawning season represent part of the area under the normal curve. If the peak spawning date is known (even approximately) each cruise can be equated to some percentage of the area under a standard normal curve. Then each cruise spawning estimate (P_i) can be used to obtain an annual spawning estimate (P_a):

$$\frac{P_i \cdot t_i}{x_i \cdot d_i} = P_a \quad (8)$$

where x_i = the proportion of the area under the normal curve represented by cruise i

t_i = the number of days included in cruise i

d_i = the duration (days) of the egg stage during cruise i .

Saville (1956, 1964) did not discuss use of the technique if more than a single cruise is included in the spawning season, but because each cruise can provide an independent estimate of annual spawning, it was possible to get as many as three estimates of round herring annual egg production within a spawning season.

Potential Yield to a Fishery

Alverson and Pereyra (1969) and Gulland (1971, 1972) have proposed that an estimate of potential yield for an unfished stock can be obtained if the virgin biomass and natural mortality coefficient are known. The estimator is:

$$C_{\max} = XMB_0 \quad (9)$$

where C_{\max} = the maximum sustainable yield
 X = a constant, assumed to be 0.5 (Gulland 1971).

M = the natural mortality coefficient. It is equal to Z , the total mortality coefficient, in an unfished stock.

B_0 = the virgin biomass. My biomass estimates of round herring are estimates of B_0 because there is no significant fishing at this time.

No estimates of M are available for round herring. It seems probable that it must lie in the range 0.4-1.0, based on literature on other relatively short-lived tropical and warm temperate clupeid stocks (Beverton 1963; Schaaf and Huntsman 1972; Dryfoos et al. 1973) and from the empirical relationship of M to life span given by Tanaka (1960). Assuming M is between 0.4 and 1.0, a range of potential yields to a fishery can be predicted. I used this approach for round herring.

Larval Abundance and Mortality

As a first step in determining survival rates of round herring larvae for comparisons among years and to determine abundance of larvae by length classes, larval abundance was estimated for each 1-mm length class:

$$P_{al} = \sum_{i=1}^r D_i \sum_{j=1}^k \frac{c_{jl}z_j}{v_j} \cdot A_j \quad (10)$$

where P_{al} = the annual estimate of total larvae in a length class l ; this is the estimate if no correction is made for night-day variation in catches

c_{jl} = the catch of larvae in length class l at station j on cruise i

z_j = the depth of tow (in meters) at station j on cruise i

v_j = the volume filtered (in cubic meters) at station j on cruise i

A_j = the area (in square meters) represented by station j on cruise i

k = the number of stations sampled during cruise i

D_i = the number of days represented by cruise i (for details, see definition under Equation (4))

r = the number of cruises upon which the estimate is based.

Larval abundance estimates are subject to errors due to escapement of small larvae through the meshes and due to avoidance of the gear by larger larvae (Smith and Richardson in press). Avoidance usually is greater during daylight than at night. Some of the avoidance error can be corrected if the differential between night and day catches of larvae in each length class is evaluated. Catches of round herring larvae were examined from each station for 1971-73 cruises. The ratios of the sum of larvae estimated under 10 m² of sea surface caught at night stations to the sum of larvae estimated under 10 m² of sea surface caught at day stations were determined for each 1-mm length class. These ratios were then used to derive functions that corrected the day-caught larval abundance estimates. Thus, abundance of larvae in each 1-mm length class at stations occupied during daylight was corrected by a factor R :

$$P_{jl} = \frac{c_{jl}z_j}{v_j} R \cdot A_j \quad (11)$$

where P_{jl} = the number of larvae in length class l in the area represented by station j

R = the factor by which the number of larvae in length class l at station j should be multiplied to correct for night-day variation. It equals 1.0 for stations sampled at night.

c_{jl} , z_j , v_j , and A_j are defined in Equation (10).

R is greater than 1.0 if avoidance is more pronounced during daylight hours. The corrected station catches (from Equation (11)) were substituted into Equation (10) for larvae caught at stations occupied during daylight. Corrected larval abundance estimates (P_{al}) were then obtained.

Larval mortality rates can be determined and expressed in terms of age if the growth rate of larvae is known or if a model of growth during the larval stage can be used to describe growth adequately. Smith and Richardson (in press)

recently have discussed the problem of obtaining crude mortality rates of larval fishes. A range of possible mortality estimates for round herring egg and larvae stages has been obtained which is useful for year to year comparisons and for comparison with larval mortality estimates that have been published on other species. Growth rates of round herring larvae are unknown and could not be determined from the data. But, from my experience in laboratory culture of clupeid larvae, an exponential model describes growth reasonably well during the larval stage. Ahlstrom (1954) and Nakai and Hattori (1962) assumed that exponential growth was valid in determining survival rates of California sardine, *Sardinops caeruleus*, and Japanese sardine, *S. melanosticta*, larvae. From laboratory rearing experiments it is evident that mean daily growth increments (\bar{b}) of clupeid larvae range from 0.3 to 1.0 mm (Houde 1973b), the increments depending on such factors as temperature and food concentration. Using this basic information, the probable mortality rates of round herring larvae from hatching until 16.0 mm SL (standard length) were estimated for the 1971-72 and 1972-73 spawning seasons.

Using a computer program several variables were considered and then the instantaneous mortality coefficient was calculated for larvae based on predetermined combinations of values of the variables. The following procedure was used:

- 1) For each designated mean daily growth increment (\bar{b}), an instantaneous growth coefficient (g) is calculated.

$$a) \quad t = \frac{L_t - L_0}{\bar{b}} \quad (12)$$

where t = the time in days to grow from L_0 to L_t at a mean daily growth increment \bar{b}

L_t = the maximum length of larvae considered to adhere to the exponential growth model (usually 20.0 mm SL)

L_0 = the minimum length of larvae to be considered in calculating the instantaneous growth coefficient (g). (This value was 4.1 mm SL for round herring.)

$$b) \quad g = \frac{\log_e L_t - \log_e L_0}{t} \quad (13)$$

where g = the instantaneous growth coefficient. A different value of g results from each

value of \bar{b} that is submitted to the program.

- 2) The annual spawning estimate (P_a) for a given spawning season and the larval abundance estimates by 1-mm length classes, corrected for night-day variation (P_{a1}) are entered.
- 3) The duration (in days) of each class from 2) above is determined:
 - a) The egg: Duration is arbitrarily assigned, based on knowledge of developmental stages in plankton collections or from laboratory rearing experiments. For round herring in the eastern Gulf of Mexico it is 2.0 days.
 - b) Nonfully vulnerable length classes: Duration is arbitrarily assigned, usually by submitting a range of possible values in the program. Larvae in these length classes are underrepresented in catches because of escapement through the meshes, and are not considered in subsequent mortality estimation.
 - c) Fully vulnerable length classes.

$$D_i = \frac{\log_e L_B - \log_e L_A}{g} \quad (14)$$

where D_i = duration of the class (in days)

L_B = upper boundary of length of a size class

L_A = lower boundary of length of a size class

g is defined in Equation (13).

- 4) The mean age of each class is then estimated:
 - a) The egg: Mean age is arbitrarily assigned. (It is one-half the assigned duration.)
 - b) Nonfully vulnerable length classes: Mean age is assigned. It equals duration of the egg stage plus one-half the duration of nonfully vulnerable length classes.
 - c) The mean age of fully vulnerable length classes.

$$T_A = \text{duration of the egg stage} + \text{duration of nonfully vulnerable length classes} + \frac{\log_e L_b - \log_e L_a}{g} \quad (15)$$

where L_b = the midpoint of the length class under consideration

L_a = the smallest length larva considered to be fully vulnerable to the gear

g is defined in Equation (13).

- 5) Abundance estimates for each class are corrected for duration. This is necessary to estimate the number present at mean age in that class. If exponential growth holds, the number of larvae in each successive age group will have been underestimated before the duration correction was made, because the time spent by larvae in successive length classes is decreasing. The correction is made by dividing the abundance estimates of each class (including the egg stage) from step 2 above by their durations, given in step 3.
- 6) The instantaneous mortality coefficient is then calculated for each combination of mean daily growth increment, assigned egg stage duration, and assigned nonfully vulnerable larvae duration. It is estimated from the exponential regression of night-day-corrected and duration-corrected abundances on mean age and is fitted for all age-classes that were adequately represented in the data, excluding nonfully vulnerable larvae. For round herring the regression was fit for age-classes including the egg stage and larvae ranging from 4.1 to 16.0 mm SL.

$$N_t = N_0 \exp(-Zt) \quad (16)$$

where Z = the instantaneous coefficient of rate of decline in catch. It is the instantaneous mortality coefficient if factors such as gear avoidance are not significant contributors to the decline in catch as larvae grow older

N_t = the number of eggs or larvae at time t

N_0 = the y -axis intercept; it is an estimate of abundance at time 0 (i.e., the number of eggs that was spawned)

t = the time (in days) from spawning.

- 7) Mortality with respect to length also is estimated in the exponential regression of night-day-corrected abundance on length. Only fully vulnerable length classes were used in this calculation. For round herring, larvae from 4.1 to 16.0 mm SL were included in the analysis.

$$N_L = N_A \exp(-ZL) \quad (17)$$

where Z = the instantaneous coefficient of rate of decline in catch. It is the instantaneous mortality coefficient per millimeter of standard length if factors such as gear

avoidance do not contribute significantly to decline in catch as larvae grow.

N_L = the number of larvae of length L

N_A = the y -axis intercept

L = the standard length (millimeters) of larvae.

RESULTS

Occurrence of Eggs and Larvae

Eggs and larvae of round herring were collected on cruises from November to May (Table 1), and were most common in January and February. They did not occur in cruises from June through September, indicating that there is no spawning during summer in the eastern Gulf of Mexico. Most eggs and larvae were collected on the outer continental shelf (Figure 2) where depths ranged from 30 to 200 m. Eggs occurred on only two occasions at stations less than 30 m deep and on a single occasion at a station deeper than 200 m (Figure 2), although relatively little sampling effort was made at stations beyond the 200-m depth contour. Occurrences of larvae were more widespread (Figure 2), as expected due to dispersal by water currents, but most occurrences remained within the 30- to 200-m depth zone. The observed distribution suggests that most of the adult population is found on the outer shelf, at least during the spawning season. A major spawning center is located between long. 082°30' and 084°30' W and lat. 27°00' and 28°00' N (Figures 2-6). The location is about 150 km from Tampa Bay in a west by southwest direction. This is the same general area where round herring adults were trawled in exploratory fishing surveys (Anonymous 1958; Salnikov 1969). There is evidence that a second minor spawning center is found between long. 082°00' and 083°30' W and lat. 24°45' and 25°30' N. This location is just north of the Dry Tortugas Islands.

The cruise means for numbers of round herring eggs under 10 m² ranged from 0.00 to 151.20 for the 17 cruises in the survey (Table 1). Considering only positive stations (i.e., stations where round herring eggs were collected on a cruise), cruise means ranged from 8.30 to 604.81 under 10 m² of sea surface (Table 1). Catches at individual stations frequently ranged from 11 to 1,000 under 10 m² but exceeded 1,000 on only three occasions during the 17 cruises (Figures 3-6). Round herring

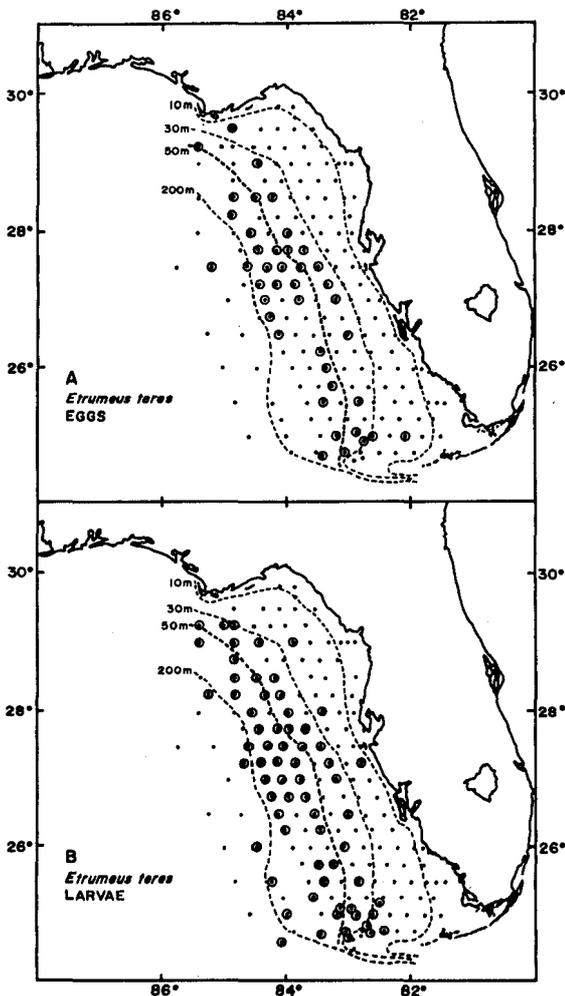


FIGURE 2.—A.) Stations in the survey area where eggs of round herring were collected at least once during 1971-74. Stations where eggs did not occur are indicated by dots. B.) Stations in the survey area where larvae of round herring were collected at least once during 1971-74. Stations where larvae did not occur are indicated by dots.

egg abundances for each cruise at all stations, as well as summaries for other clupeid species, have recently been reported (Houde et al. 1976).

Cruise means for round herring larvae ranged from 0.00 to 20.29 under 10 m² (Table 1). At positive stations the cruise means for larvae ranged from 4.44 to 175.07 under 10 m² (Table 1), but the latter value was based on a single positive station for cruise CL 7412. Excluding that cruise, the highest mean larval abundance under 10 m² at positive stations was 49.97. No stations had more than 1,000 larvae under 10 m² during the 17 cruises. Tabulated station data on catches and

abundance of round herring, and other clupeid larvae, have been published (Houde et al. 1976).

The survey area did not encompass the entire spawning area of round herring in the eastern Gulf. Eggs were collected at stations located farthest offshore on some cruises (Figures 3-6) but abundance was less at stations deeper than 200 m than at shallower stations. I believe that most of the spawning area and spawning population was included in the survey area, and that my egg abundance estimates suffer only small biases because of failure to sample a part of the population.

There was no apparent difference in the intensity of round herring spawning at stations between 30 and 50 m deep compared with stations deeper than 50 m. The log₁₀ mean abundance estimates of eggs under 10 m² of sea surface for all positive stations ≤50 m and for those >50 m were calculated from pooled data of all cruises that had round herring eggs. The ≤50 m log₁₀ mean was 1.6351 ($n = 25, S_x = 0.1609$); the >50 m log₁₀ mean was 1.5585 ($n = 32, S_x = 0.1209$). These means did not differ significantly (t -test; $P > 0.50$). However, the area between the 30- and 50-m depth contours was less than that included between the 50- and 200-m contours. The total area between the 30- and 200-m depth contours was considered to be the spawning area; 40.1% of the area is in the 30- to 50-m zone while 59.9% is between 50 and 200 m. Thus, the total abundance of eggs in the area where depths exceeded 50 m probably was greater than abundance in shallower areas. The 50-m depth contour divides the shelf area in the eastern Gulf into approximate halves. For eight cruises in which sampling effort was distributed nearly equally to include potential spawning area in water ≤50 m and >50 m (cruises 8C 7113-TI 7114, 8B 7132-TI 7131-GE7127, 8B 7201-GE 7202, GE 7208, IS 7209, IS 7303, IS 7308, and IS 7320), the summed totals of egg abundance from the areas represented by stations on these cruises were compared with respect to the 50-m depth contour. A total abundance of 11.92×10^{11} eggs was estimated for stations ≤50 m; total abundance was 16.73×10^{11} at deeper stations. If these egg abundance estimates reflect relative adult abundance, then 41.6% of the adult population was located in depths ≤50 m and 58.4% was distributed at depths >50 m. The total abundance of eggs, and apparently of adult round herring, is directly proportional to the surface area of the two depth zones. Some small fraction of the spawning population inhabited depths greater than those sampled in

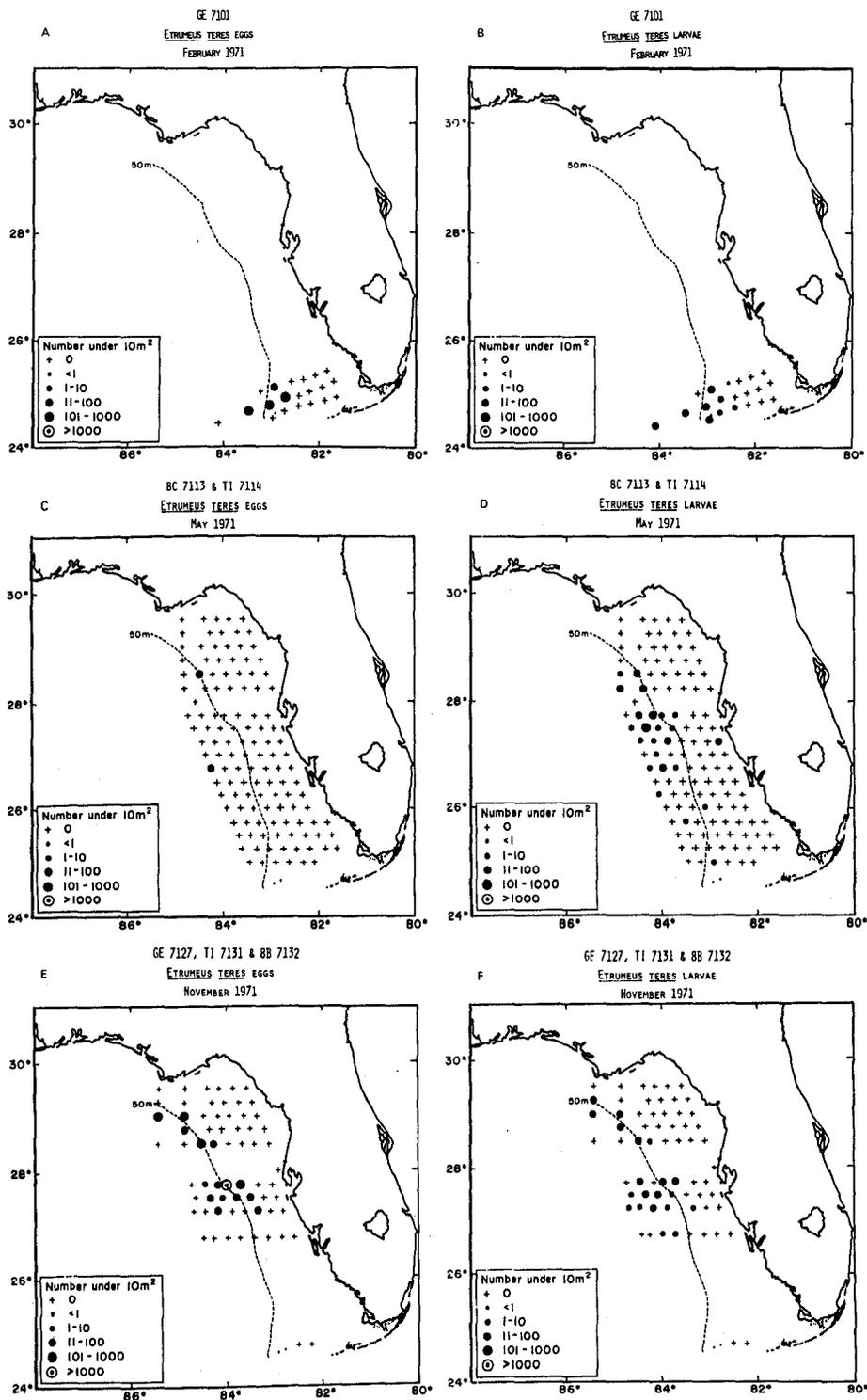


FIGURE 3.—Distribution and abundance of round herring eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface. A, B: Cruise GE 7101, February 1971. C, D: Cruise 8C 7113-TI 7114, May 1971. E, F: Cruise GE 7127-TI 7131-8B 7132, November 1971.

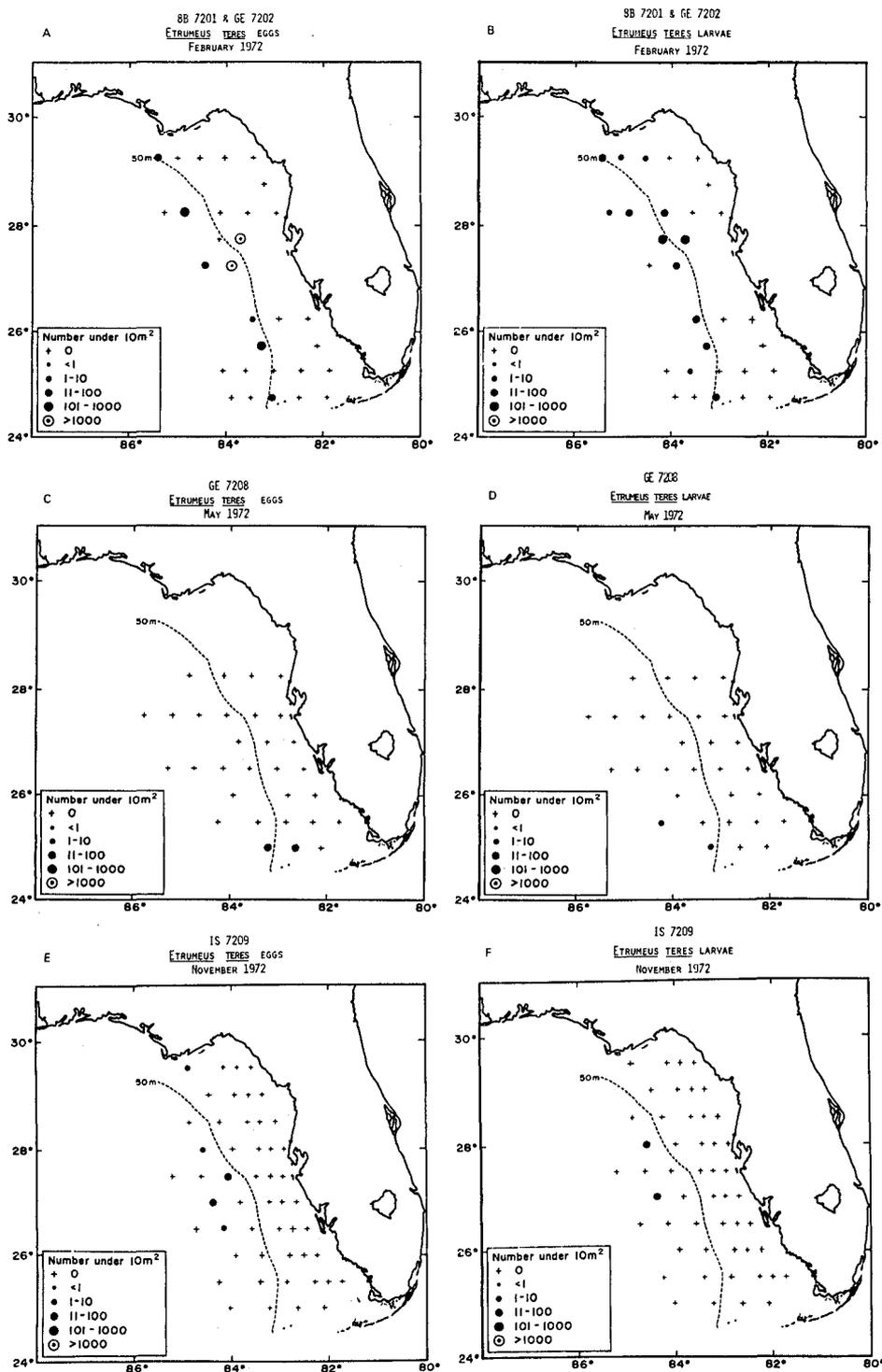


FIGURE 4.—Distribution and abundance of round herring eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface. A, B: Cruise 8B 7201-GE 7202, February 1972. C, D: Cruise GE 7208, May 1972. E, F: Cruise IS 7209, November 1972.

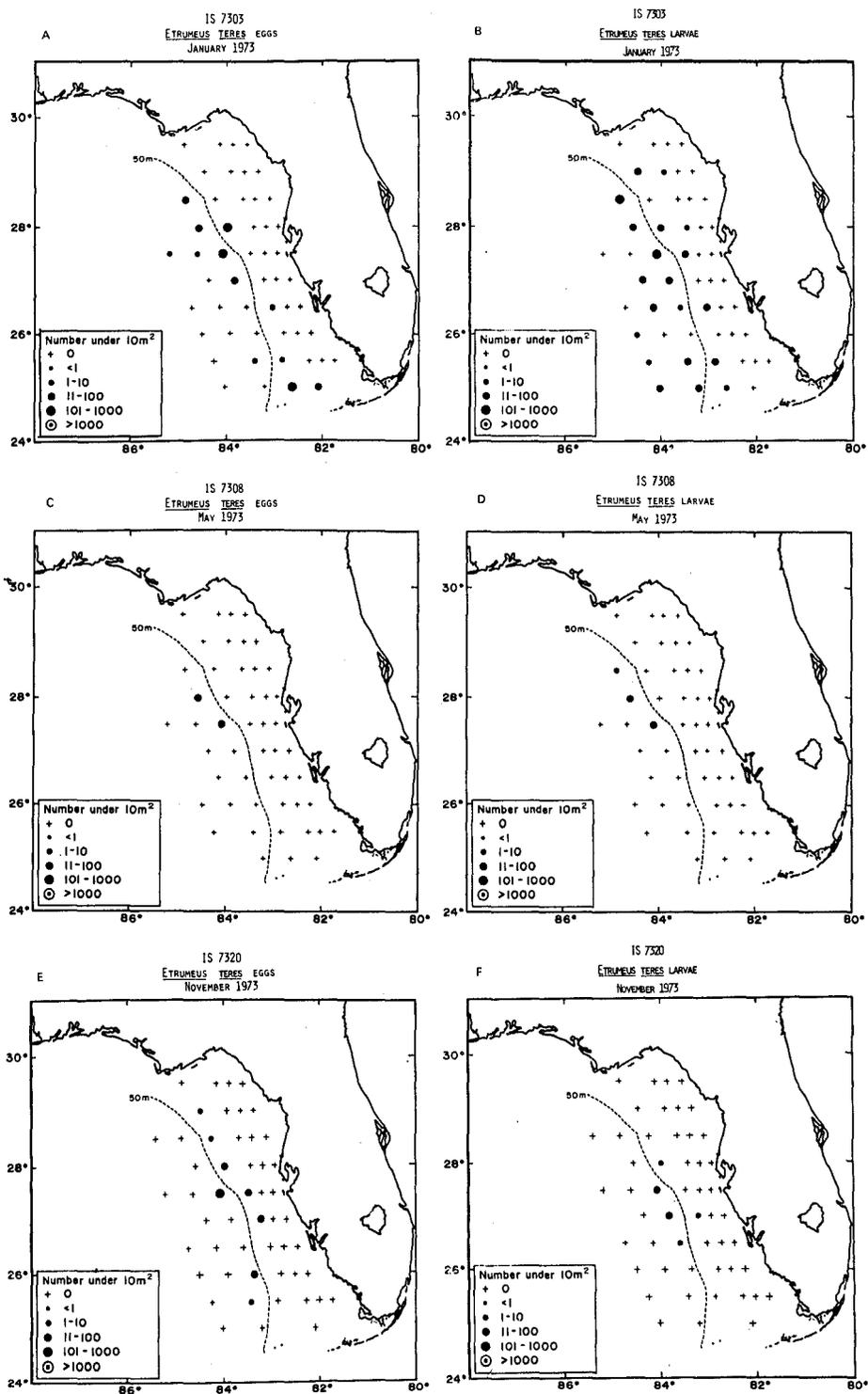


FIGURE 5.—Distribution and abundance of round herring eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface. A, B: Cruise IS 7303, January 1973. C, D: Cruise IS 7308, May 1973. E, F: Cruise IS 7320, November 1973.

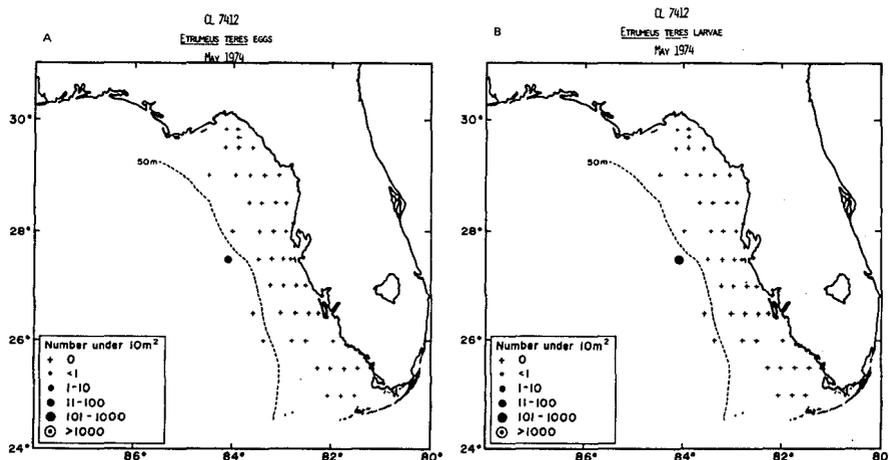


FIGURE 6.—Distribution and abundance of round herring eggs and larvae on cruise CL 7412, May 1974. Catches are standardized to numbers under 10 m² of sea surface.

our survey and the relative abundance of adults in water >50 m deep may be higher than the estimated 58.4%. Because the intensity of spawning was the same in depths, ≤ 50 and >50 m, adults apparently are not more abundant per unit of sea surface in deeper water but their greater abundance reflects the larger area of habitat suitable for round herring where shelf waters are >50 m deep.

Temperature and Salinity Relationships

Round herring eggs were collected when surface temperatures ranged from 18.4° to 26.9°C. They occurred at surface salinities of 34.50-36.50‰. Because no vertically stratified tows of the Bongo sampler were made, the percentage of eggs or larvae that occurred in surface waters is unknown. Surface temperatures from November to May were 0°-3°C higher than those at 50 m when vertical sections along transects at three latitudes were examined for each cruise in which round herring eggs or larvae were collected. Surface salinities differed by less than 0.5‰ from those at 50 m depth, except on cruise IS 7320 when surface salinities ranged from 0.6 to 1.0‰ less than those at 50 m. It is reasonable to believe that surface temperatures and salinities are representative of conditions where pelagic eggs were incubated and where larvae were found. Salinity may not be an important factor affecting spawning since the range of surface salinities at which eggs were collected nearly encompasses the entire range of

salinities found in offshore waters of the eastern Gulf. Larvae ≤ 5.0 mm SL are from 0 to about 6 days old. They occurred where surface temperatures ranged from 20.5° to 26.9°C and surface salinities from 34.10 to 36.80‰.

The percentage cumulative frequency distributions (Figure 7) of stations where eggs or ≤ 5.0 -mm larvae occurred in relation to temperature and salinity were examined. For eggs, 82.5% of the occurrences were between 21° and 26°C surface temperature, while 87.2% of the ≤ 5.0 -mm larvae occurrences were in that temperature range. Only 10.5% of the egg occurrences were at stations where surface temperatures exceeded 26°C and only 6.4% of the ≤ 5.0 -mm larvae occurrences were at such stations. The distribution of egg occurrences in relation to temperature was similar in the 1971-72 and 1972-73 spawning seasons. In 1971-72, 78.3% of the eggs occurred at stations where surface temperatures were less than 25°C; in 1972-73, 79.0% of the occurrences were at temperatures below 25°C. Comparable data were not available for the 1973-74 spawning season.

More than 50% of round herring eggs and ≤ 5.0 -mm larvae were collected at stations where surface salinity exceeded 36.00‰ (Figure 7). For eggs, considering all years' data, 79.7% of the occurrences were at surface salinities from 35.50 to 36.50‰; for ≤ 5.0 -mm larvae, 80.0% of the occurrences were in that salinity range. In 1971-72, 88.0% of the egg occurrences were at stations with surface salinities from 35.50 to 36.50‰; in 1972-

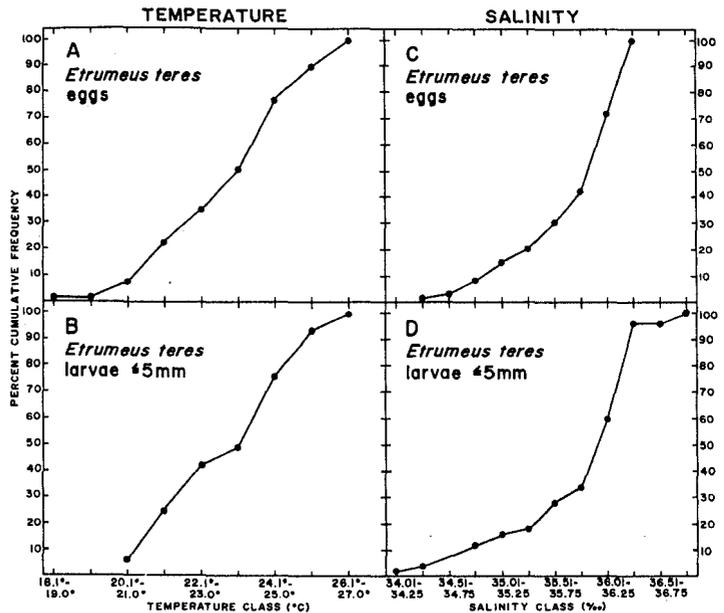


FIGURE 7.—Percent cumulative frequency distribution of 1971-74 stations where round herring eggs occurred in relation to surface temperatures (A) and to surface salinity (C), and ≤ 5.0 -mm SL larvae occurred in relation to surface temperature (B) and surface salinity (D).

73, 94.7% of the egg occurrences were in that salinity range. There were seven egg occurrences at less than 35.50‰ surface salinity on cruise IS 7320 (November 1973). This cruise influenced the cumulative frequency distribution of egg occurrences in relation to salinity (Figure 7) over all years. Data for the entire 1973-74 spawning season were not available to compare occurrence of eggs in relation to salinity with 1971-72 and 1972-73 data; but, the frequency distribution apparently would have been shifted to lower salinities in that year, reflecting low surface salinities that prevailed in the eastern Gulf in fall 1973.

Egg and Larvae Abundance in Relation to Zooplankton

There was no apparent relationship between zooplankton volumes and round herring egg or larvae abundance. Zooplankton volumes (cubic centimeters/1,000 m³ strained) were determined at each station for cruises in 1972 through 1974. Round herring egg abundance and larvae abundance were examined in relation to zooplankton volume for stations included in those cruises but the correlations were not significant.

Fecundity and Maturity

A total of 71 adult round herring was examined,

of which 39 were males and 32 were females. Based on this sample, the sex ratio did not differ significantly from 1:1 ($\chi^2 = 0.69$; $0.25 < P < 0.50$). Sixty-five specimens, from 93 to 165 mm SL, were collected in the Gulf of Mexico in August and November 1974. The 59 specimens more than 100 mm SL were maturing or near ripe. Six additional females, from 157 to 160 mm SL, that were collected in June 1973 off the east coast of Florida (lat. 30°20'N) were examined. Those six specimens were spent, the ovaries containing only small, clear, nucleated oocytes.

Ripening females usually have two modes of yolked oocytes (but occasionally only one), which apparently are both spawned during a single spawning season. Planktonic eggs were collected only from November through May. The spawning season extends from approximately 15 October to 31 May in the eastern Gulf of Mexico.

The fecundities of eight near-ripe females, 130-165 mm SL, were estimated, based on yolked oocytes present in ovaries (Table 3). Fecundities ranged from 7,446 to 19,699 and increased with size of the females. Relative fecundity (ova per gram body weight) ranged from 150 to 428 ova/g, the mean being 296.5 ova/g ($S_{\bar{x}} = 33.7$ ova/g). There was no apparent relationship between relative fecundity and either length or weight of females. The mean relative fecundity estimate, 296.5 ova/g, was used in subsequent adult biomass determinations. If all yolked oocytes were not

TABLE 3.—Fecundity estimates and related data from eight female round herring collected in the Gulf of Mexico, November 1974.

Specimen	Standard length (mm)	Weight (g)	Ovary weight (g)	Gonad index ¹ (%)	Ovary sample weight (g)	Number ova in sample	Fecundity (ova)	Relative fecundity (ova/g)
1	165	55.60	1.13	2.03	0.030	523	19,699	354
2	138	34.82	0.36	1.03	0.025	709	10,210	293
3	152	44.41	0.41	0.92	0.025	454	7,446	168
4	149	40.65	1.10	2.71	0.035	553	17,380	428
5	161	55.20	0.60	1.09	0.020	276	8,280	150
6	143	37.97	0.43	1.13	0.025	781	13,433	354
7	130	29.62	0.65	2.19	0.035	535	9,936	335
8	144	37.28	0.33	0.89	0.025	818	10,798	290

¹Gonad index is the ratio of ovary weight to weight of the female, expressed as a percentage.

spawned in a spawning season, the estimate of relative fecundity is too high and biomass estimates are low. Because no modes of yolked oocytes remained in ovaries of spent females from the June collection, I believe that yolked oocytes were spawned and that biomass estimates were not biased by this possible source of error.

Ito (1968) estimated mean fecundity of Japanese round herring to be 9,212 ova. His estimates were based only on the most advanced mode of yolked oocytes, although two modes usually were present. Ito's estimates are lower than the estimated fecundities of Gulf of Mexico round herring. Also, the diameters of near-ripe ova that he reported averaged 1.4 mm which is greater than that for spawned eggs in the Gulf of Mexico which average only 1.29 mm in diameter (Houde and Fore 1973). Diameters of ovarian ova reported by Ito (1968) are not in accord with those reported for pelagic eggs of Japanese round herring by Uchida et al. (1958), who gave the diameter as 1.25 mm. The length at first maturity, which Ito observed to be approximately 170 mm SL in Japanese specimens, exceeded that of my specimens by about 70 mm.

Time Until Hatching

Duration of the egg stage from spawning until hatching was estimated indirectly from the occurrence of three distinct embryonic stages during cruise IS 7303, at stations where surface temperatures were 21°-22°C. Spawning by round herring takes place at night, and early embryonic stages were collected only between midnight and 0400 e.s.t. Two other distinct embryonic stages were collected during those hours, one of which was a full-term embryo that was about to hatch. I assumed 2200 e.s.t. to be the peak spawning time. The time from spawning to hatching is approximately 2.1 days at 21°-22°C. Watson and Leis (1974) reported that Hawaiian round herring eggs

incubated approximately 2 days when surface temperatures were in the range 23°-25°C.

The value of 2.0 days was used for hatching time in subsequent abundance estimation procedures (Equations (4), (5), and (8)). It probably overestimates duration for cruises during fall and spring, but it is a good estimate for the winter season when most spawning occurs. Overestimating duration would result in an underestimate of daily spawning and an underestimate of adult biomass. Because there were no data on duration of the egg stage for fall and spring cruises, I chose to accept a possible small bias of underestimating round herring biomass. O'Toole and King (1974) incubated South African round herring eggs at 11°-20.5°C. The eggs had been collected in plankton tows when surface temperature was 16.5°C. They estimated that round herring eggs hatched in 135 h at 11°C and 36 h at 20.5°C. They assumed that the blastodermal cap stage eggs, with which they began experiments, were only 4-6 h old. Gulf of Mexico round herring probably do not spawn at the low temperatures that O'Toole and King observed in South African waters. Temperatures as low as 16.5°C during the spawning season in the Gulf of Mexico occurred only at depths of 150 m and greater, on the outer edge of the continental shelf. Also, the rate of development of Gulf of Mexico eggs at temperatures above 20°C apparently is slower than that of South African eggs.

Cruise Egg Abundances

The estimated abundances of round herring eggs present in areas represented by each cruise are given in Table 4. Egg abundances, including all developmental stages, ranged from 0.24 to 209.31×10^{10} for cruises during the spawning season. No round herring eggs (or larvae) were collected on cruise CL 7405. That cruise was made

TABLE 4.—Abundance estimates of round herring eggs for each cruise. Estimates were obtained using Equations (2) and (3), and are not corrected for duration of the egg stage.

Cruise	Area represented by the cruise (m ² × 10 ³)	Positive area ¹ (m ² × 10 ³)	Cruise egg abundance (eggs × 10 ¹⁰)
GE 7101	25.79	13.69	6.08
8C 7113			
TI 7114	120.48	21.80	0.24
GE 7117	101.10	0.00	0.00
8C 7120			
TI 7121	189.43	0.00	0.00
GE 7127			
8B 7132			
TI 7131	72.99	21.58	25.26
8B 7201			
GE 7202	148.85	78.43	209.31
GE 7208	124.88	15.79	1.51
GE 7210	48.43	0.00	0.00
IS 7205	104.59	0.00	0.00
IS 7209	149.80	17.79	1.37
IS 7303	149.80	78.19	38.49
IS 7308	151.42	10.52	4.04
IS 7311	156.50	0.00	0.00
IS 7313	153.18	0.00	0.00
IS 7320	153.89	31.34	6.33
CL 7405 ²	52.00	0.00	0.00
CL 7412	91.33	2.91	0.62

¹Positive area is defined as the area representing stations where either eggs or larvae of round herring were collected.

²No stations on this cruise were located far enough offshore for round herring egg or larvae to have been collected.

during the spawning season, but because only nearshore stations were sampled, the round herring spawning area was not included in the cruise area. Abundance estimates in Table 4 are based on Equations (2) and (3). Cruise abundance estimates for eggs were used to estimate adult biomass in following sections.

Adjusting Cruise Egg Abundance Estimates

The cruise egg abundance estimates were adjusted for cruises GE 7127-TI 7131-8B 7132 and GE 7208. On these two cruises only a part of the round herring spawning area was sampled (Figures 3, 4). For cruise GE 7127-TI 7131-8B 7132 only 0.655 of the potential round herring spawning area was included, and for GE 7208 only 0.839

of the area was included. Abundance estimates for each of those cruises were adjusted by dividing the cruise egg abundance estimates (Table 4) by their respective area factors (0.655 or 0.839). Adjusted cruise egg abundance estimates are: (GE 7127-TI 7131-8B 7132)— 38.56×10^{10} ; (GE 7208)— 1.80×10^{10} . The effect of adjusting egg abundance for these cruises had a minor effect on biomass estimation. Biomasses based on the adjusted and unadjusted egg abundance estimates were calculated and are compared in subsequent sections.

Annual Spawning and Biomass Estimates

Method I

The cruise abundance estimates (Table 4) were adjusted for duration of the egg stage by dividing each estimate by 2.0 days, the estimated time from spawning until hatching, to give estimates of daily spawning during each cruise (Table 5). Daily spawning estimates for each cruise were then expanded by Sette and Ahlstrom's (1948) method to a representative number of days (D_i defined in Equation (4)) in the spawning season of 15 October to 31 May (Table 5). Variance estimates on cruise and annual egg abundance were then obtained (Equations (4) and (6)). Finally, the estimated adult biomass was calculated (Equation (7)) (Table 5).

Estimates of biomass were obtained for 1971-72 and 1972-73 when sampling was carried out over the entire spawning seasons. Estimated biomass was 717,815 metric tons in 1971-72 but only 131,136 metric tons in 1972-73 (Table 5). The variance estimates are relatively low, but because only three cruises were made within the round herring spawning season and no estimates of day to day variation in spawning are available, there is a large source of unaccounted variation. The

TABLE 5.—Annual spawning and biomass estimates for round herring from the eastern Gulf of Mexico during the 1971-72 and 1972-73 spawning seasons. Estimates are based on the Sette and Ahlstrom's (1948) technique.

Spawning season	Cruise	Daily spawning estimate (eggs × 10 ¹¹)	Days represented by cruise	Eggs spawned during cruise period (× 10 ¹¹)	Variance estimates on spawned eggs (× 10 ²⁴)	Adult biomass (metric tons)
1971-72	GE 7127					
	TI 7131					
	8B 7132	1.928	71.0	136.888	10.245	
	8B 7201					
	GE 7202	10.466	88.0	921.008	206.576	
	GE 7208	0.090	70.0	6.300	3.717	
Annual total			229	1,064.196	220.538	717,815
1972-73	IS 7209	0.069	64.5	4.451	1.787	
	IS 7303	1.925	91.0	175.175	34.470	
	IS 7308	0.202	73.5	14.847	4.100	
Annual total			229	194.473	40.357	131,136

number of days representing each cruise is large and spawning almost certainly was not uniform within each cruise period. This may account for the more than fivefold difference in biomass estimated during the 2 yr. On the other hand it is possible that biomass did differ greatly between the 2 yr. This is especially possible because the eastern Gulf may be an open-ended system with regard to round herring habitat. Round herring eggs and larvae were abundant in the north-central Gulf (Fore 1971) indicating that a large adult population is present there. If a single population of round herring inhabits the Gulf, the part found in the eastern Gulf might vary from year to year.

The area adjustments that had been made for two 1971-72 cruises, to account for part of the spawning area not being sampled, affected the biomass estimate in that spawning season. Without adjustments the biomass estimate was 685,273 metric tons rather than 717,815 metric tons. The effect of adjustment was to raise the estimate by more than 32,500 metric tons. This is only a 4.7% increase in estimated biomass.

It is unlikely that round herring biomass is as great as 1 million metric tons in the eastern Gulf of Mexico, but it probably is considerably in excess of 100,000 metric tons. Confidence limits, at the 0.95 probability level, based on the annual spawning variance estimates (Table 5) placed the probable range of round herring biomass between 517,470 and 918,160 metric tons in 1971-72 and between 45,430 and 216,840 metric tons in 1972-73.

Method II

The daily spawning estimates for each of the three cruises during 1971-72 and 1972-73 were plotted against their cruise middates (Figure 8). Areas under the resulting polygons were determined and were equated to annual spawning (Table 6). This method is like that outlined by Simpson (1959). Biomasses were calculated using Equation (7).

Biomass estimates were 698,045 metric tons in 1971-72 and 130,995 metric tons in 1972-73 (Table 6). These estimates are similar to those obtained by Method I.

Method III

If spawning follows a normal distribution during the period 15 October to 31 May, then each

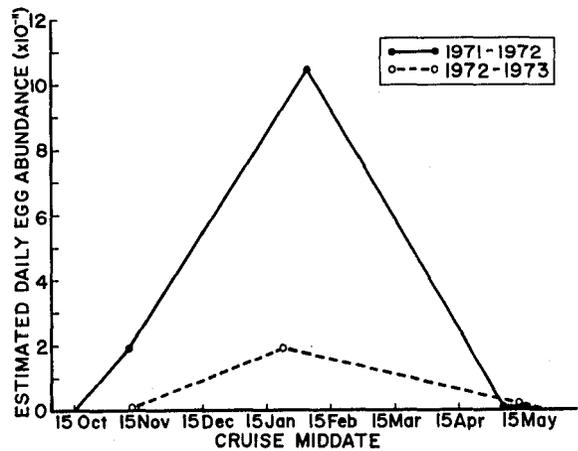


FIGURE 8.—Round herring egg abundance estimates in the eastern Gulf of Mexico based on three cruises in 1971-72 and 1972-73. Each symbol represents the estimated daily spawning at the middate of a cruise. The area enclosed by the polygons is an estimate of the total spawning by round herring during each of the seasons.

TABLE 6.—Annual spawning and biomass estimates for round herring from the eastern Gulf of Mexico during 1971-72 and 1972-73 spawning seasons. Estimates are based on the method described by Simpson (1959).

Spawning season	Cruise	Daily spawning estimate (eggs $\times 10^{11}$)	Annual spawning estimate (eggs $\times 10^{11}$)	Adult biomass (metric tons)
1971-72	GE 7127			
	TI 7131			
	8B 7132	1.928		
	8B 7201			
	GE 7202	10.466		
	GE 7208	0.090	1,034.852	698,045
1972-73	IS 7209	0.069		
	IS 7303	1.925		
	IS 7308	0.202	194.200	130,995

cruise within that 229-day period can be represented as some proportion of the area under a normal curve with standard deviation of 38.17 days. Saville (1956, 1964) discussed use of the technique for a single cruise near the peak of the spawning season, but I have applied it (Equation (8)) to eight representative cruises during four round herring spawning seasons (Table 7). The observed variation within a season on annual spawning and biomass estimates is great. Although spawning is heaviest near the middle of the spawning season (Figure 8), it probably does not follow the normal distribution closely. It seems that in most years spawning intensity increases rapidly to near peak level during late November and then gradually decreases during spring months. Deviations from normality would cause large estimating errors, especially for cruises that

TABLE 7.—Annual spawning and biomass estimates for round herring from the eastern Gulf of Mexico during 1970-71 through 1973-74 spawning seasons. Estimates are based on the method of partitioning the spawning season into component parts of the normal curve (Saville 1956). The spawning season is assumed to be 229 days in length, ranging from 15 October to 31 May.

Spawning season	Cruise	Proportion of area under normal curve	Daily spawning estimate (eggs $\times 10^{11}$)	Days included in cruise	Annual spawning estimate (eggs $\times 10^{11}$)	Adult biomass estimate (metric tons)
1970-71	8C 7113					
	TI 7114	0.0057	0.012	12	25.270	17,046
1971-72	GE 7127					
	TI 7131					
	8B 7132	0.0081	1.928	11	2,618.258	1,766,110
	8B 7201					
	GE 7202	0.1153	10.466	11	998.436	673,481
	GE 7208	0.0072	0.090	10	125.310	84,526
Mean					1,247.335	841,373
1972-73	IS 7209	0.0072	0.069	9	85.592	57,735
	IS 7303	0.0857	1.925	9	202.109	136,330
	IS 7308	0.0041	0.202	9	443.798	299,358
Mean					243.833	164,474
1973-74	IS 7320	0.0067	0.316	9	425.198	286,811

were not made near the middle of the spawning season.

Mean biomass estimates for the 1971-72 and 1972-73 seasons were 841,373 and 164,474 metric tons, respectively (Table 7). These estimates do not differ much from those obtained by Methods I and II (Tables 5, 6). Also, it is interesting to note that the midwinter estimates in the 1971-72 (673,481 metric tons) and 1972-73 (136,330 metric tons) seasons, each based on a single cruise, gave estimates of round herring biomass nearly identical to those obtained by Methods I and II. A single cruise in January or February, with a subsequent biomass estimate by Method III, seems to be as good for obtaining estimates of round herring biomass as three cruises spaced over the entire spawning season. Multiple cruises within the November through February peak spawning period would, of course, be the best approach to gain precision in estimating biomass of this species from spawning surveys.

The annual spawning estimates, based on Method III from the eight cruises (Table 7), are log-normally distributed and an estimate of the mean biomass present from 1970 to 1974, with confidence limits at the 0.95-probability level, was calculated based on the eight \log_{10} egg abundance estimates. Geometric mean annual spawning estimate for 1970-74 was $2,685.11 \times 10^{10}$ and the confidence limits are: $P(792.08 \times 10^{10} \leq P_a \leq 9,103.32 \times 10^{10}) = 0.95$. Expressed in terms of biomass, the geometric mean was 181,120 metric tons with confidence limits, $P(53,429 \leq B \leq 614,052) = 0.95$. If the arithmetic mean of the eight biomass estimates is considered a valid estimate of mean biomass, its value is 415,175 met-

ric tons. A reasonable conclusion is that round herring biomass in the eastern Gulf is less than 1 million metric tons but probably greater than 100,000 metric tons.

Concentration of Biomass

The largest positive areas (i.e., areas where either round herring eggs or larvae were collected) occurred in cruises 8B 7201-GE 7202 and IS 7303 when more than $78 \times 10^9 \text{ m}^2$ were in that category. This is nearly equivalent to the $76.5 \times 10^9 \text{ m}^2$ in the survey area between 30- and 200-m depths that was determined by planimeter. The biomass of adult round herring is primarily located in the 30- to 200-m depth zone. If the confidence limits on biomass, based on Method I, are considered then biomass per unit area of sea surface must have been between 67.6 and 120.0 kg/hectare in 1971-72 and between 5.9 and 28.3 kg/hectare in 1972-73.

Potential Yield to a Fishery

Using Equation (9), the potential yield to a fishery, C_{\max} , can be estimated, based on the range of biomass estimates that is available. Although the natural mortality coefficient, M , is not known, it probably lies between 0.50 and 1.00 for round herring in the eastern Gulf of Mexico. The estimated values of C_{\max} if M equals 0.50, 0.75, or 1.00 are given in Table 8.

Potential yield estimates range from 32,749 to 420,687 metric tons (Table 8). The best estimates almost certainly lie midway between the extremes, so that 50,000-250,000 metric tons are in

TABLE 8.—Range of potential yield estimates for eastern Gulf of Mexico round herring, based on biomass estimates by three methods. Yields are predicted at three possible values of M , the natural mortality coefficient. Biomass estimates were obtained from values in Tables 5-7.

Biomass estimating method and spawning season	Biomass estimate (metric tons)	Estimated potential annual yields (metric tons) for given values of M		
		$M = 0.5$	$M = 0.75$	$M = 1.0$
I 1971-72	717,815	179,454	269,181	358,908
I 1972-73	131,136	32,784	49,176	65,568
I Mean of 1971-72 and 1972-73	424,476	106,119	159,179	212,238
II 1971-72	698,045	174,511	261,767	349,022
II 1972-73	130,995	32,749	49,123	65,498
II Mean of 1971-72 and 1972-73	414,520	103,630	155,445	207,260
III 1971-72 mean	841,373	210,343	315,515	420,687
III 1972-73 mean	164,474	41,118	61,678	82,237
III 1971-72 cruises 8B 7201 and GE 7202	673,481	168,370	252,555	336,740
III 1972-73 cruise IS 7303	136,330	34,082	51,124	68,165
III 1970-74 geometric mean of 8 estimates	181,120	45,280	67,920	90,560
III 1970-74 arithmetic mean of 8 estimates	415,175	103,794	155,691	207,588

the range that I believe represents the mean potential annual yield of the stock. This is equivalent to a potential harvestable yield of 6.5-32.7 kg/hectare in the 76.5×10^9 m² of round herring habitat in the eastern Gulf. If stock size fluctuates greatly from year to year then the harvestable yield also may vary. As Alverson (1971) has pointed out, the biological potential yield is not necessarily the realizable yield. The realizable yield will depend upon the availability of the stock and its vulnerability to fishing gear. Neither of these factors has been evaluated for eastern Gulf round herring. It is possible that large year to year fluctuations in round herring biomass do occur, as suggested by the great differences in 1971-72 and 1972-73 biomass estimates. Such variation could reflect year class fluctuations or yearly changes in distribution of parts of the stock between the north-central and eastern Gulf. Although they are abundant, there is no reason to believe that round herring in the eastern Gulf constitute a stock as large as the Gulf menhaden stock in the north-central Gulf of Mexico, which produces a mean annual yield of more than 550,000 metric tons.

Larval Abundance Estimates

Larvae occurrence and abundance varied seasonally in the same manner as eggs (Table 9). The range of larvae abundances for positive cruises, including larvae in all length classes, was $0.47-31.95 \times 10^{10}$. In subsequent estimates of larval

TABLE 9.—Abundance estimates of round herring larvae for each cruise. Estimates include larvae in all size classes and were obtained using Equations (2) and (3).

Cruise	Area represented by the cruise (m ² × 10 ⁹)	Positive area ¹ (m ² × 10 ⁹)	Cruise larvae abundance (larvae × 10 ¹⁰)
GE 7101	25.79	13.69	2.58
8C 7113			
TI 7114	120.48	21.80	3.60
GE 7117	101.10	0.00	0.00
8C 7120			
TI 7121	189.43	0.00	0.00
GE 7127			
TI 7131			
8B 7132	72.99	21.58	2.92
8B 7201			
GE 7202	148.85	78.43	26.55
GE 7208	124.88	15.79	0.47
GE 7210	48.43	0.00	0.00
IS 7205	104.59	0.00	0.00
IS 7209	149.80	17.79	2.70
IS 7303	149.80	78.19	31.95
IS 7308	151.42	10.52	3.99
IS 7311	156.50	0.00	0.00
IS 7313	153.18	0.00	0.00
IS 7320	153.89	31.34	1.71
CL 7405 ²	52.00	0.00	0.00
CL 7412	91.33	2.91	5.09

¹Positive area is defined as the area representing stations where either eggs or larvae of round herring were collected.

²No stations on this cruise were located far enough offshore for round herring eggs or larvae to have been collected.

abundance by length classes and in mortality estimation procedures, larval abundance by each 1-mm length class was adjusted for cruises GE 7127-TI 7131-8B 7132 and GE 7208 to account for only part of the potential round herring spawning area having been sampled. The adjustment factors were 0.655 and 0.839, the same factors that were used to adjust egg abundance for those cruises.

Larvae that were collected ranged from 2.1 to 30.0 mm SL during the survey. Length frequencies of larvae in the 2.1-20.0 mm SL range are illustrated in Figure 9. Larvae >20.0 mm were rarely collected during the survey. Frequencies for each length class in Figure 9 are given as estimated abundance during each cruise (Equation (3)). No area adjustments have been made in Figure 9 for the two cruises that did not cover the entire spawning area. Round herring larvae <4.0 mm SL usually were in poor condition, with curved or deformed bodies, and their measurements are underestimates of true length. O'Toole and King (1974) hatched eggs that they had collected and reported that preserved, newly hatched round herring larvae were 3.75-4.00 mm long. The 4.1- to 5.0-mm SL length class was the most abundant class in my survey (Figure 9). I assumed that this length class was fully vulnerable to the sampling gear, although some escapement may have occurred for larvae of this size.

The ratios of night-caught to day-caught larvae

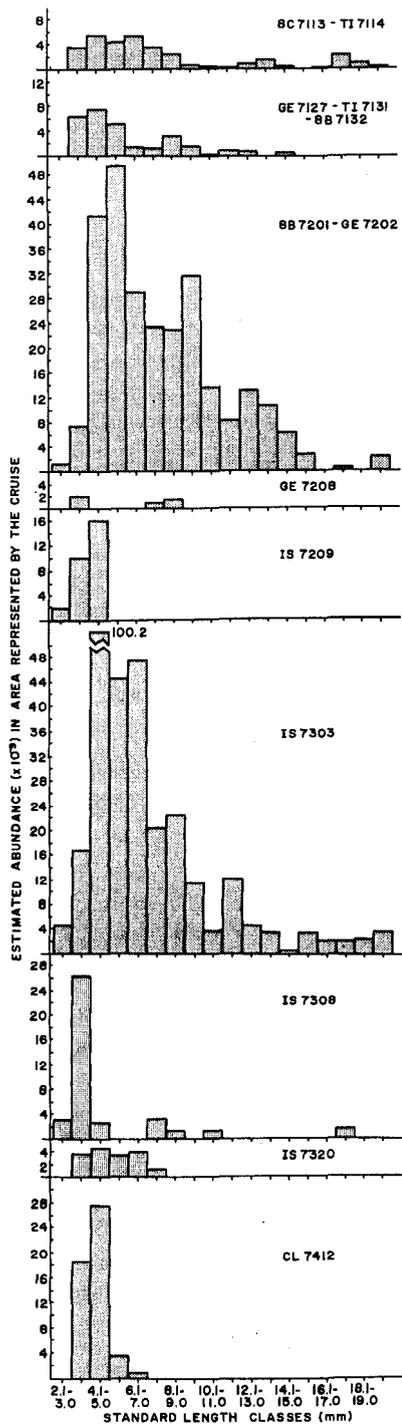


FIGURE 9.—Length-frequency distributions of round herring larvae for 1971-74 cruises to the eastern Gulf of Mexico. Frequencies are expressed as estimated abundance of larvae in each length class within the area represented by the cruise.

by length classes were examined over all cruises and they indicated that considerable net avoidance was occurring in the day relative to that occurring at night. The data were plotted by 2-mm length classes (Figure 10), and functions were fitted to allow estimation of the night-caught to day-caught ratio for larvae in any length class. The ratio increased rapidly for larvae of 4.0-13.0 mm, but then decreased from a factor of more than 3.0 to about 1.0 when larvae had grown to 18.0 mm. Two power functions were fitted: for larvae 2.1-14.0 mm SL the function was $R = 0.3041 X^{0.9115}$, where R is the ratio of night-caught to day-caught larvae and X is standard length of larvae; for 12.1- to 20.0-mm SL larvae the function was $R = 44,521.54 X^{-3.7298}$. Larva catches made at daytime stations were adjusted by R (Equation (11)). Exponential functions or a single polynomial could have been used in place of the power functions to describe the relationship, but the power functions provided reasonably good fits to the data and were acceptable for correction purposes. No adjustments were made for larvae <4.0 mm or >18.0 mm because there was no observable difference in night or day catches for larvae of those lengths.

The round herring larvae night to day catch ratios are unusual with respect to the observed

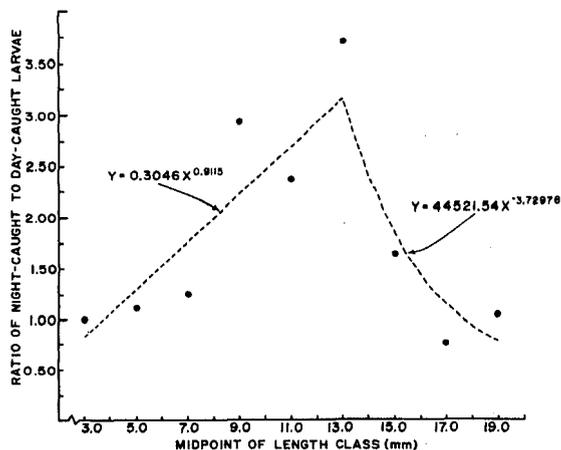


FIGURE 10.—Night to day ratios of sums of catches, standardized to numbers under 10 m² of sea surface, for round herring larvae collected in 1971-73 in the eastern Gulf of Mexico. The ratios were calculated for larvae within each 2-mm length class from 2.1 to 20.0 mm SL. Fitted power functions describe the relationships for larvae from 2.1 to 13.0 mm SL and for larvae from 13.1 to 20.0 mm SL. Larval abundance estimates for each length class at stations occupied during daylight were corrected by the appropriate ratio factor for each length class to account for daytime avoidance.

decrease in the ratio for larvae >13.0 mm. The ratio increased in other studies on clupeoid larvae throughout the size range of larvae that were collected (Ahlstrom 1954, 1959b; Lenarz 1973; Matsuura in press), and this is true for other species of clupeid larvae that I have studied in the Gulf of Mexico. The return of the ratio toward unity after round herring larvae reached 13.0 mm must indicate that larvae 13.0-18.0 mm became as good at avoiding the gear at night as during the day. The alternative explanation, which seems unlikely, is that larger larvae lost the potential to avoid the gear during daylight. Daylight is only one factor that could allow larvae to avoid the gear and adjustment of catches to account for it can only partially correct for avoidance losses. The correction was made, however, in an attempt to get the best estimate possible for round herring larval mortality during the 1971-72 and 1972-73 seasons.

Larval abundance estimates, corrected for daytime avoidance, were determined by 1-mm length classes for the 1971-72 and 1972-73 seasons (Figure 11) (Equation (10)). Except for larvae in the 4.1- to 5.0-mm length class, which were twice as abundant in 1972-73, total abundance of larvae was similar in the two seasons. The greater abundance of 4.1- to 5.0-mm larvae in 1972-73 could have reflected the reduction in towing speed from the previous season. Escapement of small larvae through the meshes may have been more important in 1971-72 when towing speed averaged about 0.7 knot faster.

Abundance of round herring larvae decreased exponentially as lengths increased during each season (Figure 11). Fitted exponential functions for 5.1- to 16.0-mm larvae in 1971-72 and 4.1- to 16.0-mm larvae in 1972-73 provided estimates of the instantaneous mortality coefficients per millimeter increase in length (Figure 11). The coefficients were $Z = 0.2269$ in 1971-72 and $Z = 0.3647$ in 1972-73. These correspond to percentage losses per millimeter increase in length of 20.3% in 1971-72 and 30.5% in 1972-73. Confidence intervals at the 0.95 probability level were $Z = 0.2269 \pm 0.0930$ in 1971-72 and $Z = 0.3647 \pm 0.1179$ in 1972-73. The null hypothesis of no difference in mortality coefficients between years was accepted at the $\alpha = 0.05$ probability level (t -test; $0.05 < P < 0.10$), but the t value was close to the rejection region suggesting that mortality may have been higher in 1972-73 than in 1971-72.

The mortality coefficients that I obtained are

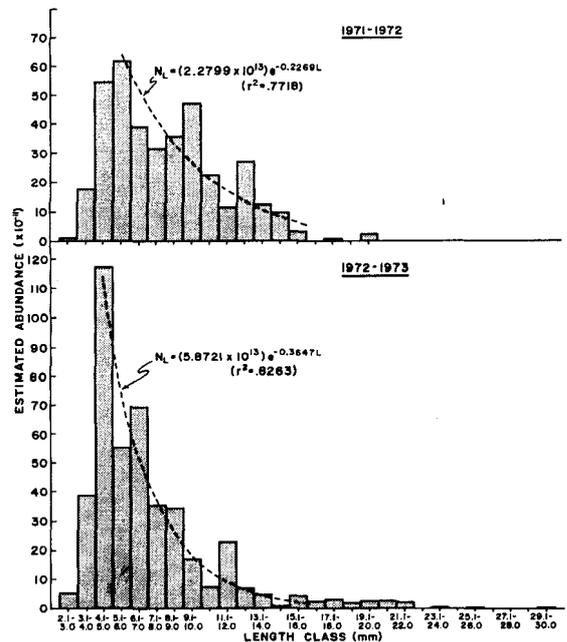


FIGURE 11.—Length-frequency distributions of annual larval abundance estimates of round herring larvae collected in the eastern Gulf of Mexico. Frequencies in each 1-mm length class are expressed as estimated annual abundance and have been corrected for daytime avoidance. Fitted exponential functions provide estimates of the instantaneous coefficient of decline in abundance by length, the 1971-72 and 1972-73.

similar to those reported by Lenarz (1973) from several years of data on Pacific sardine and northern anchovy, *Engraulis mordax*. He reported a range of instantaneous coefficients of 0.15-0.33, averaging 0.22 for Pacific sardine, that correspond to a 20% loss per millimeter of growth. For anchovy his instantaneous coefficients ranged from 0.32 to 0.46, averaging 0.39, a mean decrease of 32% per millimeter of growth. Matsuura (in press) has measured the rate of decline in catches of Brazilian sardine, *Sardinella brasiliensis*, obtaining an instantaneous coefficient of 0.4962, corresponding to a 39% decrease in catch per millimeter of growth. Most of the decline in catch of larger round herring larvae presumably was due to larval mortality but gear avoidance also must be important. For this reason mortality curves were fitted only for larvae 16.0 mm or less in length. Catches of larger larvae were sporadic and possibly greatly influenced by gear avoidance.

Larval mortality is best expressed as a function of age. If it is assumed that growth of round herring larvae is exponential from the post yolk-sac

stage to 20.0 mm SL, then the instantaneous mortality coefficients, based on mean estimated ages of larvae, can be calculated using Equations (12)-(16). No information on growth rates of round herring larvae was available, but mean daily growth increments of other Gulf of Mexico clupeid species have been determined in laboratory rearing experiments and they range from 0.3 to 1.0 mm (Richards and Palko 1969; Saksena et al. 1972; Houde 1973b; Houde and Swanson 1975). Growth rates in those experiments exceeded 0.7 mm/day only when temperature was above 26°C. Mean daily growth of round herring larvae probably is between 0.3 and 0.7 mm. Duration of the egg stage from spawning until hatching is about 2.0 days. The duration of nonfully vulnerable length classes was estimated from a knowledge of growth rate and development times of other clupeid species that have been reared in the laboratory. Larvae of yellowfin menhaden, *Brevoortia smithi*, did not begin to grow in length until nearly 4 days after hatching at 26°C (Houde and Swanson 1975) when they were about 4.5 mm SL; larvae of *Harengula jaguana* did not grow significantly until they were nearly 3 days old and 4.5 mm SL at 26°-28°C (Houde et al. 1974). The exponential growth phase was assumed to begin in the 4.1- to 5.0-mm length class for round herring. The nonfully vulnerable length classes of 2.1-5.0 mm in 1971-72 were assigned durations that varied from 4.0 to 7.0 days; the nonfully vulnerable 2.1- to 4.0-mm length classes in 1972-73 were assigned durations of 1.5-3.0 days. Various combinations of mean daily growth increments and durations of nonfully vulnerable length classes were entered

into the program to estimate mortality in relation to age of larvae (Equations (12)-(16)) for 1971-72 and 1972-73. Examples, for one combination of values of the variables in 1971-72 and one combination in 1972-73, are provided in Table 10 and Figure 12.

Given mean daily growth increments of 0.3-0.7 mm (corresponding to instantaneous growth coefficients of 0.0299-0.0698) and the most probable durations of nonfully vulnerable length classes, the probable range of instantaneous mortality coefficients was 0.0866-0.1739 in 1971-72 and 0.0835-0.1719 in 1972-73 (Table 11). In terms of daily mortality the 1971-72 probable estimates ranged from 8.3 to 16.0%; in 1972-73 they ranged from 8.0 to 15.8%. Although the estimated range is great, it is nearly the same for the two seasons. Varying duration of the nonfully vulnerable length classes had only minor effects on mortality rate estimation (Table 11), but varying the growth rate had important effects.

The values of N_0 , the y -axis intercepts, provide yet another series of estimates of annual spawning, because they estimate the numbers of eggs present at time zero. The intercept values are generally lower than spawning estimates by the other methods and are not considered to be good estimates of spawning. It seems that the exponential model of loss fits the decrease in larval abundances reasonable well, but that a greater than expected mortality occurs between egg and fully vulnerable larval length classes. Figure 12 illustrates this possibility. If only larval mortality had been considered, rather than total mortality from egg to 16.0-mm larvae, the instantaneous coefficients

TABLE 10.—Two examples of data treated to obtain class durations and mean ages of round herring larvae from the eastern Gulf of Mexico. Abundance estimates are then corrected for duration, and the duration-corrected abundances were subsequently regressed on mean ages to obtain mortality rates (Table 11). Data are from 1971-72 and 1972-73 egg and larvae abundance estimates that were previously corrected for daytime avoidance. In these examples the mean daily growth increment (\bar{b}) was set at 0.50. The nonfully vulnerable length classes were 2.1-5.0 mm in 1971-72 with duration of 6 days, and 2.1-4.0 mm in 1972-73 with duration of 2.5 days. Calculating procedures are given in Equations (12)-(16). The regressions for these data are given in Figure 12.

Class	1971-72				Class	1972-73			
	Abundance (no. $\times 10^{11}$)	Duration (days)	Mean age (days)	Duration-corrected abundance (no. $\times 10^{11}$)		Abundance (no. $\times 10^{11}$)	Duration (days)	Mean age (days)	Duration-corrected abundance (no. $\times 10^{11}$)
Eggs	2,128.39	2.00	1.00	1,064.20	Eggs	388.94	2.00	1.00	194.47
2.1-5.0	72.90	6.00	5.00	12.15	2.1-4.0	43.89	2.50	3.25	17.56
5.1-6.0	61.96	3.26	9.52	19.00	4.1-5.0	117.78	3.98	6.37	29.58
6.1-7.0	38.96	2.76	12.87	14.11	5.1-6.0	55.29	3.26	10.39	16.95
7.1-8.0	31.70	2.39	15.74	13.24	6.1-7.0	69.81	2.76	13.75	25.28
8.1-9.0	35.92	2.11	18.25	16.99	7.1-8.0	35.42	2.39	16.62	14.79
9.1-10.0	46.88	1.89	20.48	24.77	8.1-9.0	34.55	2.11	19.13	16.34
10.1-11.0	22.29	1.71	22.49	13.02	9.1-10.0	17.08	1.89	21.36	9.02
11.1-12.0	11.60	1.56	24.32	7.41	10.1-11.0	7.44	1.71	23.37	4.34
12.1-13.0	26.81	1.44	25.99	18.63	11.1-12.0	22.99	1.56	25.20	14.70
13.1-14.0	12.25	1.33	27.53	9.19	12.1-13.0	6.67	1.44	26.87	4.63
14.1-15.0	9.89	1.24	28.97	7.97	13.1-14.0	4.79	1.33	28.41	3.59
15.1-16.0	3.31	1.16	30.31	2.85	14.1-15.0	0.74	1.24	29.85	0.59
					15.1-16.0	4.36	1.16	31.19	3.76

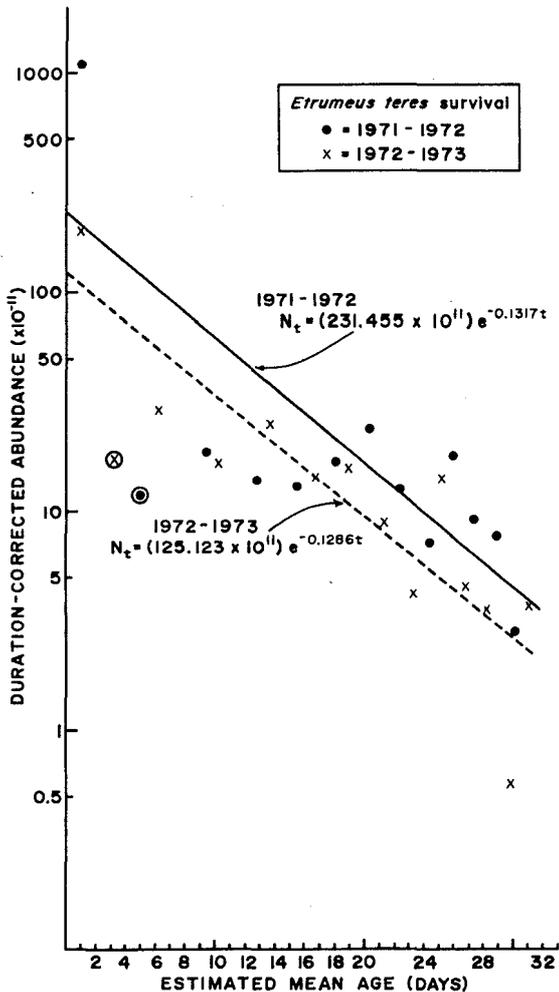


FIGURE 12.—Estimated abundance of egg and larval stages of round herring in the eastern Gulf of Mexico in 1971-72 and 1972-73. Abundance is expressed as a function of estimated age. Fitted exponential functions give estimates of the instantaneous rates of decline in abundance for eggs and larvae up to 31 days of age. The two symbols enclosed in circles represent nonfully vulnerable length classes and were not included in the regression estimates of instantaneous decline.

would have been lower. In 1971-72, $Z = 0.0563$ for fully vulnerable larval stages and $Z = 0.1123$ for those stages in 1972-73. The results suggest that egg and nonfully vulnerable larvae mortality were higher in 1971-72 than in 1972-73. Mortality of vulnerable larval stages appears to have been higher in 1972-73 when the population declined by 10.6%/day as opposed to 1971-72 when it declined only 5.5%/day. The higher mortality rate of larvae in 1972-73 also was apparent in the mor-

tality estimates based on larval lengths (Figure 11).

High mortality of eggs or newly hatched larvae may be characteristic of many clupeids, including round herring. Smith (1973) recently reported that Pacific sardine eggs experience high mortality, the instantaneous rate being $Z = 0.31$ during that stage. Pilchard, *Sardina pilchardus*, eggs undergo high mortality during early embryonic stages (Southward and Demir 1974) and embryos of *Clupeonella delicatula* suffered high mortality, especially under unfavorable temperature regimes (Pinus 1974).

The best probable estimates of mortality from the egg to 16.0-mm larval size are near the middle of the ranges given in Table 11, at instantaneous growth rates of 0.0498. In 1971-72, $Z = 0.1317$ is the most probable estimate while $Z = 0.1286$ seems most probable in 1972-73. These estimates correspond to average daily losses of 12.3% in 1971-72 and 12.1% in 1972-73. Estimates of the instantaneous mortality coefficients based on the two examples given in Table 10 and Figure 12 coincide with what I believe may be the best estimates of mortality. Confidence limits, at the 0.95 probability level, were placed on the instantaneous mortality coefficients derived from these examples. They were wide, ranging from $Z = 0.0635$ -0.1999 in 1971-72 and $Z = 0.0823$ -0.1749 in 1972-73. The coefficients $Z = 0.1317$ in 1971-72 and $Z = 0.1286$ in 1972-73 did not differ significantly between years (t -test; $P > 0.50$).

The estimates of mortality rates could be too high if avoidance by larvae was increasing significantly as they grew, reducing their probability of capture. If growth was not exponential, but linear, during the larval phase, then the mortality estimates may be too low, because duration-corrected abundances gave relatively high values to older larvae that presumably were growing through length classes at an increasing rate.

Because of the difficulty in ageing eggs or larvae of marine fishes, few estimates of mortality rates in relation to age have been reported. Ahlstrom (1954) reported that about one Pacific sardine larva survived to 21.25 mm/100,000 eggs spawned during the first 40-45 days of life, which corresponds to an instantaneous daily loss rate of 0.16-0.17. Japanese sardine was investigated by Nakai and Hattori (1962). They reported survival from egg to the 15.0 mm stage as 0.10% in 54 days, corresponding to an instantaneous rate of $Z = 0.1279$. This rate is nearly identical to that which

TABLE 11.—Summary of mortality estimates for round herring larvae from the eastern Gulf of Mexico, 1971-72 and 1972-73. Estimates were obtained from the exponential regression of egg and larvae abundances on mean age. Instantaneous growth and mortality coefficients were calculated for various possible combinations of mean daily growth increment and duration of the nonfully vulnerable larval stages. Egg stage duration was assumed to be 2.0 days. Nonfully vulnerable larval stages were 2.1-5.0 mm SL in 1971-72 and 2.1-4.0 mm SL in 1972-73. Explanation of the estimating method is given in Equations (12)-(16).

Season	Mean daily growth increment (mm)	Instantaneous growth coefficient (g)	Nonfully vulnerable larvae duration (days)	Instantaneous mortality coefficient (Z)	Y-axis intercept, N_0 (no. $\times 10^{11}$)	Daily mortality rate, $1 - \exp(-Z)$	
1971-72	0.3	0.0299	4.0	0.0866	103.25	0.0830	
	0.3	0.0299	5.0	0.0866	112.07	0.0830	
	0.3	0.0299	6.0	0.0866	121.40	0.0830	
	0.3	0.0299	7.0	0.0866	131.21	0.0829	
	0.5	0.0498	4.0	0.1331	186.35	0.1246	
	0.5	0.0498	5.0	0.1325	208.29	0.1241	
	0.5	0.0498	6.0	0.1317	231.46	0.1234	
	0.5	0.0498	7.0	0.1307	255.74	0.1225	
	0.7	0.0698	4.0	0.1739	285.65	0.1596	
	0.7	0.0698	5.0	0.1718	324.45	0.1579	
	0.7	0.0698	6.0	0.1693	364.72	0.1558	
	0.7	0.0698	7.0	0.1665	406.00	0.1534	
	1972-73	0.3	0.0299	1.5	0.0842	71.56	0.0808
		0.3	0.0299	2.0	0.0840	73.89	0.0805
0.3		0.0299	2.5	0.0837	76.26	0.0803	
0.3		0.0299	3.0	0.0835	78.68	0.0801	
0.5		0.0498	1.5	0.1303	114.55	0.1222	
0.5		0.0498	2.0	0.1295	119.80	0.1214	
0.5		0.0498	2.5	0.1286	125.12	0.1207	
0.5		0.0498	3.0	0.1278	130.52	0.1200	
0.7		0.0698	1.5	0.1719	160.03	0.1580	
0.7		0.0698	2.0	0.1702	168.78	0.1565	
0.7		0.0698	2.5	0.1683	177.58	0.1549	
0.7		0.0698	3.0	0.1665	186.39	0.1533	

is most probable for round herring larvae. Harding and Talbot (1973) and Bannister et al. (1974) reviewed the results of several years' investigations on plaice, *Pleuronectes platessa*. They found that instantaneous mortality coefficients varied from only 0.0209 to 0.0685 from egg stage 1 to larval stage 4 during the long larval life of more than 150 days. Mortality of haddock eggs and larvae was reported by Saville (1956), who gave a series of estimates that ranged from 4 to 16%/day ($Z = 0.04-0.17$) during a 4-yr survey of egg and larvae abundance at Faroe. Jack mackerel, *Trachurus symmetricus*, larvae have a high rate of mortality (Lenarz 1973), losses ranging from 57 to 67% per millimeter of growth. Farris (1961) reported mortality of jack mackerel larvae in relation to age. The instantaneous mortality rate, calculated from his data, was 0.23 during the first 30 days of life. Mortality of Japanese mackerel, *Scomber japonicus*, larvae was very high (Watanabe 1970), 99.95% mortality having occurred between the egg and 15-mm larval stage in about 23 days. This corresponds to an instantaneous rate of $Z = 0.3295$. Round herring larval mortality rates apparently are similar to those of other clupeoids from temperate or subtropical marine waters (Ahlstrom 1954; Nakai and Hattori 1962; Lenarz 1973). On average they are slightly higher

than those reported for haddock (Saville 1956). Round herring larvae have mortality rates that are much higher than those reported for North Sea plaice larvae and lower than those reported for jack mackerel or Japanese mackerel larvae.

If any period can be considered critical in the early life of round herring, it must occur between the time that eggs are spawned and when larvae reach 5.5 mm long. Greatest losses occurred at that time in 1971-72 and 1972-73 (Figure 12). Abundance estimates declined by more than 92% between the egg and 5.5-mm larvae in 1971-72. A decline of more than 78% in abundance was estimated between egg and 5.5-mm larvae in 1972-73 (Table 12, Figure 12). For larvae longer than 5.5 mm mortality decreased, the decrease in rate being especially great in 1971-72.

The number of survivors and percentage survival of round herring larvae at various stages were estimated (Table 12) from the number of spawned eggs obtained by Method I and the information on growth and mortality that is summarized in Table 11. The Method I spawning estimate was assumed to be a better estimate of initial number of eggs than the y-intercept estimates in Table 11. There was an apparent high mortality between spawning and hatching which exceeded 75% in 1971-72 (Table 12). The larval populations were reduced by

TABLE 12.—Estimated numbers and percentages of survivors of round herring larvae at hatching, 5.5 mm SL and 15.5 mm SL in 1971-72 and 1972-73. Estimates are made for three possible growth rates (see Table 11). Duration of the nonfully vulnerable larval stages was set at 6.0 days for 2.1-5.0 mm larvae in 1971-72 and 2.5 days for 2.1-4.0 mm larvae in 1972-73. The number of spawned eggs in each year was based on estimates by Method I (Table 5). Predicted numbers at hatching, 5.5 mm and 15.5 mm are calculated from exponential functions based on Table 11 data.

Season	Instantaneous growth coefficient (g)	Number of spawned eggs ($\times 10^{11}$)	Instantaneous mortality coefficient (Z)	Number hatching ($\times 10^{11}$)	% mortality to hatching ¹	Number of 5.5-mm larvae ($\times 10^{11}$)	% mortality to 5.5 mm	Number of 15.5-mm larvae ($\times 10^{11}$)	% mortality to 15.5 mm
1971-72	0.0299	1,064.20	0.0866	102.09	90.3	48.77	95.4	2.43	99.8
	0.0498	1,064.20	0.1317	177.86	83.3	66.06	93.8	4.27	99.6
	0.0698	1,064.20	0.1693	259.96	75.6	78.40	92.6	6.35	99.4
1972-73	0.0299	194.47	0.0837	64.51	66.8	23.00	88.2	1.26	99.3
	0.0498	194.47	0.1286	96.74	50.3	32.89	83.1	2.27	98.8
	0.1683	194.47	0.1683	126.83	34.8	41.00	78.9	3.37	98.3

¹Hatching assumed to occur at 2.0 days.

more than 99.4% at 15.5 mm in 1971-72 and by more than 98.3% in 1972-73. The 15.5-mm stage would be attained at about 31 days if the instantaneous growth coefficient was 0.0498 (equal 0.5-mm mean daily growth increment). At that growth rate, approximately 4 larvae/1,000 eggs spawned in 1971-72 and 12 larvae/1,000 eggs spawned in 1972-73 would have survived to 15.5 mm and 1 mo of age.

SUMMARY

1) Surveys of eggs and larvae were used to investigate spawning, to determine adult stock size, and to study aspects of the early life history of round herring in the eastern Gulf of Mexico during 1971-74.

2) Spawning takes place from mid-October to the end of May between the 30- and 200-m depth contours. About 60% of the total spawning occurred at depths greater than 50 m. Most spawning apparently occurred during January and February.

3) Eggs occurred when surface temperatures ranged from 18.4° to 26.9°C, and surface salinities from 34.5 to 36.5‰. Larvae ≤ 5.0 mm SL were collected when surface temperatures were from 20.5° to 26.9°C, and surface salinities from 34.1 to 36.8‰. Of the eggs 82.5% and of the ≤ 5.0 -mm larvae 87.5% were collected when surface temperatures were from 21° to 26°C. More than 50% of the eggs and ≤ 5.0 -mm larvae were collected where surface salinity exceeded 36.0‰.

4) There is a major spawning area between lat. 27°00' and 28°00'N and long. 083°30' and 084°30'W. The center of the area is located about 150 km west by southwest of Tampa Bay in depths of 50-200 m.

5) The fecundity of eight round herring females 130-165 mm SL ranged from 7,446 to 19,699.

Mean relative fecundity was 296.5 ova/g ($S_x = 33.7$). Gonads of round herring collected from August to November were ripening or near ripe. Those collected in June were spent. The sex ratio of 71 round herring adults did not differ significantly from 1:1.

6) The time from spawning to hatching, based on observations of development stages in planktonic eggs, was about 2.0 days at 22°C.

7) Adult biomass was determined by three methods from data on estimated annual spawning. The Sette and Ahlstrom's (1948) and Simpson's (1959) techniques gave estimates that ranged from 130,000 to 715,000 metric tons in 1971-72 and 1972-73. The geometric mean of eight individual estimates by Saville's (1956) method was 181,200 metric tons, the arithmetic mean being 415,175 metric tons. But, the best estimates by Saville's method were from two individual cruises in midwinter. These were 673,481 metric tons in 1971-72 and 136,330 metric tons in 1972-73. Those estimates were nearly the same as estimates obtained by the other two methods. Spawning biomass apparently was higher in 1971-72 than in 1972-73.

8) The estimated concentration of biomass between the 30- and 200-m depth contours, based on the stock size estimates, was from 67.6 to 120.0 kg/hectare in 1971-72 and from 5.9 to 28.3 kg/hectare in 1972-73.

9) The annual potential yield of round herring to a fishery, if instantaneous natural mortality coefficients lie in the range 0.5-1.0, ranged from 32,750 to 420,700 metric tons. The most probable mean annual potential yield estimates are in the range 50,000 to 250,000 metric tons. This is equivalent to 6.5-32.5 kg/hectare in the 30- to 200-m depth zone.

10) Total abundance of larvae was estimated in 1971-72 and 1972-73. The 4.1- to 5.0-mm length

class was nearly twice as abundant in 1972-73 as in 1971-72. Other length classes were somewhat more abundant in 1971-72 catches.

11) Mortality rates of larvae were estimated by length and for estimated ages. For lengths, the instantaneous coefficients of decline in catches were $Z = 0.2269$ in 1971-72 and $Z = 0.3647$ in 1972-73, corresponding to 20.3 and 30.5% losses per millimeter of growth. For ages, a range of estimates of daily mortality, based on varying growth rates and nonfully vulnerable larva stage durations, was obtained. The most probable daily mortality estimates were $Z = 0.1317$ in 1971-72 and $Z = 0.1286$ in 1972-73, corresponding to percentage losses of 12.3 and 12.1% on a daily basis.

12) It is probable that more than 99.4% mortality from eggs to 15.5-mm larvae occurred in 1971-72, and that more than 98.3% mortality occurred during that period in 1972-73. About 4 larvae/1,000 eggs spawned survived to 31 days and 15.5 mm in 1971-72, while about 12 larvae/1,000 eggs survived to that stage in 1972-73.

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